

**Aggression as a personality trait in *Egernia whitii*:
mechanisms and outcomes.**



**A thesis submitted in fulfillment of the requirements for the
degree of Doctor of Philosophy**

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Declaration of originality

This thesis contains no material which has been accepted for a degree or diploma by the University of Tasmania or any other institution, and to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text of this thesis, nor does the thesis contain any material that infringes copyright.

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Statement of ethical conduct

The research associated with this thesis abides the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th edition, 2004 and the University of Tasmanian Animal Ethics Guidelines.

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Statement of Co-Authorship

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Jo McEvoy (candidate and author 1) was the primary author and conceived of the idea, executed the idea and was responsible for its presentation. David Sinn (author 2), Geoffrey M While (author 3), and Erik Wapstra (author 4) contributed to the formalization, development, refinement and presentation.

Paper 2 (Chapter 3): While, G.M., Isaksson, C., McEvoy, J., Sinn, D.L., Komdeur, J., Wapstra, E., and Groothuis, T.G.G., 2010. Repeatable intra-individual variation in

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Geoffrey M While (author 1) and Caroline Isaksson (author 2) were the primary authors and contributed to the idea, its development, execution and presentation. Candidate (author 3) conducted the field work and personality tests, conducted statistical analysis on personality measures, contributed ideas on links to animal personality, and assisted with manuscript refinement, and presentation. David L Sinn (author 4) designed and contributed to the aggression tests, assisted with refinement and presentation and offered ideas on the links to animal personality. Jan Komdeur (author 5), Erik Wapstra (author 6) and Ton GG Groothuis (author 7) contributed with development of the system, ideas and refinement of the manuscript.

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Viva la Egernia
Beware the fury.

Abstract

Behaviour mediates all aspects of an individual's life and can act as the link between ecology and evolution, influencing population dynamics and eco-evolutionary processes which affect evolutionary pathways. In the past decade, consistent intra-individual differences in behaviour, known as animal personality, have become an increasing focus of attention in behavioural ecology and evolutionary biology. However, despite this increased attention in the field, few studies have considered both the proximate mechanisms and ecological outcomes of animal personality within a single, free-living, unmanipulated population. I addressed this shortcoming in *Egernia whitii*, a social Australian skink species.

I first examined five key personality traits (aggression, boldness, exploration, activity and sociability) in *E. whitii*. I found that the structural consistency of traits varied in both a temporal and sex-specific manner, and furthermore, the majority of the traits exhibited only moderate to no intra-individual consistency. Aggression was the only trait that exhibited both structural consistency and strong intra-individual consistency over time. Based on this, and previous work in this species, I focused the remainder of this thesis on the personality trait of aggression. I examined the physiological basis of aggression to understand the proximate mechanism(s) that maintains consistent intra-individual variation in aggression and the ultimate outcomes of aggression by examining its ecological role in *E. whitii*.

Hormones and intra-individual differences in metabolism have both been proposed as key proximate physiological mechanisms that organize and maintain correlated suites of behaviour as personality traits. The sex-steroid testosterone in particular facilitates the activation of aggressive behaviour and is important for enabling individuals to mount an aggressive response to conspecific challenges in territorial/mate/offspring defense. Individual *E. whitii* displayed consistent intra-individual differences in both aggression and baseline circulating plasma testosterone concentrations. However, contrary to the majority of literature that indicates a positive relationship between aggression and testosterone, male *E. whitii* displayed a negative relationship between circulating plasma testosterone concentrations and aggression at both the baseline level and during the up-regulation of testosterone following an aggressive challenge. An aggressive challenge also resulted in a disruption of intra-individual consistency in

circulating plasma testosterone concentrations. Manipulating testosterone concentrations had no corresponding influence on either mean levels of aggression or intra-individual consistency in aggression. While in females there was no association between aggression and aspects of the oxidative stress system (they by-products of the metabolic process), there was a positive association between aggression and antioxidant capacity in males. This suggests that in males, aggression may induce an increased oxidative challenge resulting in an elevation of antioxidant defense.

In addition to examining the proximate physiological mechanisms underpinning aggression, I also examined the ecological outcomes of aggression in this species. Competition between individuals is a key component of the agonistic intrasexual interactions that influence resource acquisition, social system dynamics, and ultimately reproductive success. Traits that therefore influence success in competition should be favored in selection. Although aggression in males did not predict the outcome of competition in the laboratory, or the outcome of competition in the field (i.e. territory size, territory overlap, or reproductive output), aggression was important to males (in terms of reproductive output) when habitat quality was limited. This suggests that the importance of aggression is context dependent in male *E. whitii*. Spacing of *E. whitii* within the habitat also appears to be determined by habitat quality, with more aggressive individuals found in warmer areas. Additionally, female reproductive effort is influenced by both environmental variation and her aggressive phenotype. These results indicate important ecological outcomes to aggression in this species, with aggression influencing both territory spacing, female reproductive effort, and (in conjunction with environmental variation), male reproductive output, processes which will likely influence population, and potentially evolutionary, dynamics.

This thesis represents an integrated, holistic examination of personality in a free-living vertebrate population. It adds to the growing body of work suggesting that the relationship between testosterone and aggression is not straightforward, supports the calls for considering metabolism as a proximate underpinning of personality and indicates that the role that aggression plays in eco-evolutionary dynamics is an exciting area of further research.

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Chapter One

General Introduction

An individual's behaviour mediates all aspects of its life, from sibling competition as an infant, through dispersal as a juvenile, predator avoidance and competition over resources throughout their life, and mate choice through to parental care as an adult. Behaviour is therefore a key factor shaping an individual's social environment as well as in mediating an individual's interaction with its physical environment (Weislo 1989, Duckworth 2009, Sih et al. 2012, Wolf and Weissing 2012). As a result, behaviour can act as an evolutionary pacemaker, through inhibiting or facilitating evolutionary change (Duckworth 2009, Wolf and Weissing 2012). A high level of behavioural plasticity can act as an inhibitor of evolutionary change through shielding organisms from strong directional selection and allowing individuals to exploit new resources or move to less stressful environments. Alternatively, changes in behaviour can expose individuals to novel selection pressures and result in rapid evolution of morphological, life history and physiological traits, thus facilitating evolutionary change (Duckworth 2009). Regardless of whether behaviour acts as an inhibitor or a facilitator of evolutionary change, a shift in behaviour is a critical step in the evolutionary sequence. Specifically, a shift in behaviour has the immediate consequence of altering selection pressures faced by an individual and this affects the evolutionary process. Any behavioural trait that influences the interaction between an individual and its environment (the interim ecological outcome) therefore has the potential to be an agent of selection and result in evolutionary change.

Distinct behavioural differences, such as the alternative reproductive strategies of territory holders versus floaters seen in a variety of species (Gross 1996, Oliveira 2008), have been well characterized. In the cichlid fish (*Pelvicachromis pulcher*), for example, territorial males recruit females (harems) to their spawning site and aggressively defend territories, while non-territorial males employ satellite-sneaker strategies and try to steal fertilizations while territory owners are spawning (Martin and Taborsky 1997). Territory owners have a higher reproductive success than satellite males, but satellite males have longer lifespans. These two reproductive strategies are fixed early in ontogeny and have a strong heritable component; males

are either territory owners or satellites (Martin and Taborsky 1997). Individuals within the same species or population vary in their behavioural expression (Bell 2007a, Sih and Bell 2008, Dall et al. 2012). Where discrete behavioural differences exist, there is logical structure and consistency to the alternative behavioural strategies. This is less clear for continuous behavioural traits which have always been viewed as more (almost infinitely) flexible (Dall et al. 2012, Sih et al. 2012). However, recent research indicates that individuals display consistent intra-individual differences in both discrete and continuous behavioural traits (Gosling 2001, Sih et al. 2004a, b, Smith and Blumstein 2008) such that individuals often exhibit less plasticity than would be expected given adaptive expression with changing internal and external factors (Dall et al. 2012). This phenomenon, termed animal personality, has recently become a key target of research (Gosling 2001, Sih et al. 2004a, b, Réale et al. 2007, Sih et al. 2012, Wolf and Weissing 2012).

Animal personality is defined as consistent intra-individual differences in behaviour along a continuum. For example, an individual that is relatively more aggressive (than conspecifics) at a particular point in time, will also be (relatively) more aggressive at another point in time (i.e. an aggressive versus a docile personality trait). Similarly, an individual that is more exploratory in a novel environment will also be more exploratory when encountering novel objects in their environment (i.e. a high-exploratory versus a low-exploratory personality trait) (Sih et al. 2004a, b, Dall et al. 2004, Sih and Bell 2008, Sih et al. 2012). Recent studies have shown that animal personality appears to be ubiquitous throughout the animal kingdom (see Gosling 2001, Sih et al. 2004a, b, Bell et al. 2009, Stamps and Groothuis 2010b, Wolf and Weissing 2012) and within-individual consistency in behaviour (i.e. ‘repeatability’ of behaviour) is often high (reviewed in Bell et al. 2009).

The presence of consistent intra-individual differences in behaviour, and potential constraints in the expression of behaviour, are likely to impact the role that behaviour plays in evolutionary change. Thus, identifying and understanding both the flexibility and constraints associated with personality traits is paramount. When an individual encounters a novel environment, either through chance events or through previous behavioural decisions, the extent to which that individual is able to respond to new food resources, predators, habitat resources or potential mates will influence its

ability to survive and reproduce in the new environment (Wcislo 1989, Wolf and Weissing 2012). Flexibility of behaviour in enabling an individual to respond to its environment may facilitate (or even drive) the evolutionary process. However, the constraint on behavioural flexibility implied by personality suggests that micro-evolutionary processes associated with individual differences in the ability to respond will affect population level processes that will influence macro-evolutionary change (Duckworth 2009).

Despite the ubiquitous nature of animal personality, and the burgeoning field of research since Sih et al.'s seminal papers introducing and emphasizing the importance of animal personality almost a decade ago (Sih et al. 2004a, b), there is still much to learn about both the causes and consequences of animal personality. This is perhaps in part due to confusion in terminology and definitions, and the lack of a general framework through which to study animal personality (Réale et al. 2007, Biro and Stamps 2008, Dingemanse et al. 2010). Réale et al. (2007) distilled the variety of terms used to describe animal personality traits into five general categories that relate to separate ecological conditions (shyness-boldness, exploration-avoidance, activity, aggressiveness and sociability), and which are potentially key targets of selection. Considering animal personality through the lens of the definitions suggested by Réale et al. (2007) facilitates important questions about the ecological and evolutionary significance of personality traits. In particular, attention is focusing on the ultimate outcomes of personality differences, the ecological correlates and functional significance of personality, as well as on the proximate mechanisms that are responsible for organizing and maintaining differences in personality (Stamps and Groothuis 2010a, b).

Ecological implications of personality

There is growing awareness that personality traits (i.e. aggression, exploration), as well as correlations between personality traits, have the potential to affect key evolutionary and ecological processes (Réale et al. 2010a, b, Sih et al. 2012, Wolf and Weissing 2012). Personality is likely to influence an array of ecological and evolutionary processes, including but not limited to: species interactions; stability, resilience and persistence of populations; social evolution; speciation and ecological invasions (Dall et al. 2012, Sih et al. 2012, Wolf and Weissing 2012). Personality is

of particular relevance to population ecology as population processes are driven by species interactions and/or spatial or temporal variation in the environment (Sih et al., 2012) and individual personality differences can influence intra- and inter-species competition and influence the structure and dynamics of ecological networks (Wolf and Weissing 2012). For example, personality influences the distribution and settlement of individuals within habitats (see Duckworth 2006 and Wolf and Weissing 2012) with more social and/or less aggressive individuals being potentially more likely to congregate. Aggregations of individuals will result in environments of higher competition, the outcomes of which will be influenced by the aggressiveness of individuals. Areas of high competition will further influence prey and resource availability (affecting species interactions and community structure and function) (Duckworth 2006, Sih et al. 2012, Wolf and Weissing 2012). Personality traits can therefore influence a suite of key individual and population level processes which are likely to drive both the ecological and evolutionary trajectories of populations (Réale et al. 2010, Dall et al. 2012, Sih et al. 2012, Wolf and Weissing 2012).

Personality influences the way in which an individual interacts with its environment, thus determining the selection pressures that the individual faces by affecting their mortality and reproductive output (Réale and Festa-Bianchet 2003, Biro et al. 2004, Dingemanse et al. 2004, Boon et al. 2007, Boon et al. 2008, Wolf and Weissing 2012). For example, bolder and/or more exploratory individuals will more readily explore a new environment, disperse further, or more quickly return to a feeding patch following a predation-scare event than shyer or less exploratory individuals and thus will gain greater access to resources (see Biro and Stamps 2008, Boon et al. 2008, Smith and Blumstein 2008, Réale et al. 2010b). Activity and aggression have also been linked to fitness outcomes. For example, activity in female red squirrels (*Tamiasciurus hudsonicus*) is correlated to her offspring's growth rate, and her aggressiveness correlated to offspring survival over-winter (Boon et al. 2007). However, these benefits also come with costs; bolder and more exploratory individuals suffer higher predation rates, more aggressive individuals are more likely to suffer injuries, and more active individuals expend more energy (see Smith and Blumstein 2008).

Importantly, the presence of animal personalities can help to explain apparently maladaptive or sub-optimal behaviour when personality traits are correlated across contexts (Dall et al. 2004, Pruitt et al. 2008, Sih et al. 2004a, b). Correlations between traits across contexts, such as high aggressiveness towards conspecifics being related to high exploration tendency, or within traits across contexts, such as individuals demonstrating high aggression towards same-sex conspecifics also demonstrating high aggression towards potential mates, are referred to as behavioural syndromes (Sih et al. 2004a, b, Wolf and Weissing 2012). Pruitt et al. (2008) demonstrated the potential importance of behavioural syndromes in a study involving aggression in the socially polymorphic spider (*Anelosimus studiosus*). Social individuals were less aggressive towards conspecifics and caught less prey than their asocial counterparts. Asocial individuals, on the other hand, were aggressive towards prey resulting in higher prey capture rates and superfluous killing, but this behaviour carried-over into courtship contexts resulting in high rates of sexual cannibalism and decreased reproductive success (Pruitt et al. 2008). Thus, individual variation in personality traits may persist because there are both costs and benefits associated with personality traits so that individuals that perform apparently sub-optimally along one behavioural gradient may out-perform individuals in another, or there are fluctuating selection pressures maintaining personality differences (Réale and Festa-Bianchet 2003, Dingemanse et al. 2004, Both et al. 2005, Smith and Blumstein 2008).

Selection pressures associated with individual variation in behaviour will vary both spatially and temporally, which can help explain the maintenance of behavioural variation within populations (Smith and Blumstein 2008). For example, while activity and aggression in female red squirrels were correlated with fitness outcomes in terms of offspring growth and survival, the magnitude and direction of the correlations among personality traits and fitness differed between years and was dependent on environmental variables (Boon et al. 2007; see above). Active females had offspring with faster growth rates in years of high food availability, but lower offspring growth rates in years of low food availability. Fluctuating selection pressures associated with environmental variation therefore maintain both high and low activity types in the population (Boon et al. 2007, see also fast vs. slow exploring great tits (*Parus major*), reviewed in Groothuis and Carere 2005). Similarly, life-history trade-offs can act to maintain different personality types within the same population. While bolder

individuals may enjoy greater access to resources, they also often suffer increased predation costs (Stamps 2007, Wolf et al. 2007, Smith and Blumstein 2008) and exploratory behaviour, while potentially enabling an individual to gain access to resources increasing both growth/survival and fecundity, will prove costly in terms of increased energy expenditure and time that could be spent on other activities (Stamps 2007). There is thus a trade-off between current and future events that may promote the maintenance of personality differences (Wolf et al. 2007).

Personality can influence how individuals cope with predictable and stochastic environmental variation and consequently how animal populations evolve (Dingemanse et al. 2004, Both et al. 2005, Dingemanse and Réale 2005, Bolnick et al. 2011). For example, populations harboring different personality types may be less vulnerable to environmental change (Bolnick et al. 2011, Wolf and Weissing 2012), and personality differences can influence population productivity, stability, co-existence and ecosystem process (Sih et al. 2012, Wolf and Weissing 2012). This is because different personality types respond differently to environmental change. For example, slow-exploring great tits respond more readily to environmental change than fast-exploring individuals as they are more sensitive and respond more quickly to changes in their environment as well as being better able to cope with social stress (see Both et al. 2005 and references therein). Differences in boldness, habitat/resource-use and competitive ability buffer population responses to changing predation pressures, habitat and resource quality, and competitive regimes respectively (Wolf and Weissing 2012) and these differences in personality can cascade throughout communities to affect eco-system wide process (Bolnick et al. 2011). Populations of Trinidadian guppies (*Poecilia reticulata*) which display consistent intra-individual differences in diet use, cause the divergence of ecosystem structure (algal, invertebrate, and detrital standing stocks) and function (gross primary productivity, leaf decomposition rates and nutrient flux) (see Bassar et al. 2010). Additionally, the mix of personality traits within a population can affect the dynamics, stability and persistence of that population (Wolf and Weissing 2012). A number of studies have suggested that personality-dependent dispersal success will influence selection on a variety of additional phenotypic traits that impact population growth and survival, and ultimately the evolutionary trajectory of populations

(Bremner-Harrison et al. 2004, Duckworth 2006, Duckworth and Badyaev 2007, Cote et al. 2010, Wolf and Weissing 2012).

The concept of animal personality is now being integrated into a whole series of domains in the field of behavioural ecology and evolution (Réale et al. 2010). The emerging picture is clear: personality differences can be expected to have substantial consequences for key life history traits, which will influence ecological and evolutionary processes (Wolf and Weissing 2012). While understanding the impact of personality on individuals, ecological function and evolutionary dynamics is integral to our understanding of animal personalities, it is also essential to investigate the proximate mechanisms that underlie personalities.

Proximate mechanisms of animal personality

The highly structured nature of behavioural differences due to personality traits raises interesting questions regarding the proximate mechanisms underlying these behavioural phenotypes, particularly since they are consistent throughout time and potentially across contexts (Ketterson and Nolan 1999, Duckworth 2010, Stamps and Groothuis 2010a, b, Groothuis and Trillmich 2011). Investigating the proximate mechanisms behind personality traits can provide insights into their evolution as it allows us to establish whether correlated behaviours are controlled by the same mechanisms, and thus the extent to which this might limit their independent expression and evolution (Sih, et al. 2004a, b, Duckworth and Sockman 2012). However, despite increased attention in animal personality research, the proximate mechanisms governing both the formation and maintenance of personality traits remain unclear (Dall et al. 2004, Bell 2007b, Duckworth and Sockman 2012). Much of the (limited) research regarding the development of personality, and the mechanisms underlying that development, has focused on the effects of genes on personality (Stamps and Groothuis 2010b). However, while previous research on the evolution of phenotypic traits has demonstrated the importance of additive genetic variation and genetic correlations (Dochterman and Roff 2010, Stamps and Groothuis 2010b), the expression of phenotypic traits will also be influenced by experiential factors, including both internal (physiological) and external (environmental) factors (Stamps and Groothuis 2010b, Groothuis and Trillmich 2011).

Although the study of the proximate mechanisms underlying animal personality has largely involved studying the genetic basis of personality, the genetic architecture of animal personality is still not well known (van Oers and Sinn 2011). A strong genetic basis to personality seems likely since there are genes with major effects on personality in humans, although evidence is limited in other animals (van Oers and Müller, 2010). Additionally, selection can influence personality over a few generations (Drent et al. 2003), personality has a heritable component (van Oers et al. 2005), and genetic influences, perhaps through pleiotropic effects, could explain limits of plasticity in personality (van Oers et al. 2005; see also Groothuis and Trillmich 2010). For example, van Oers et al. (2004a, b, c) demonstrated through artificial breeding experiments selecting for both high and low risk-taking in great tits that risk-taking behaviour has both a genetic basis and a heritable component. Risk-taking was also correlated with exploratory behaviour, indicating the possible genetic basis of a behavioural syndrome. Further work by Fidler et al. (2007) on the same system demonstrated that differences in high and low exploratory behaviour were associated with polymorphisms in the *Drd4* gene, a dopamine receptor gene that is associated with personality-associated variants in humans, monkeys and horses (see Fidler et al. 2007 and references therein). The similarity of the results among these diverse vertebrate taxa suggest that there is an association between *Drd4* gene polymorphism and variation in animal personality that predates the divergence of mammalian and avian lineages, and may be an association that is common across vertebrate species (Fidler et al. 2007). It also highlights the possibility of following micro-evolutionary changes in the frequencies of behaviourally relevant gene polymorphisms within populations where selection acts differentially on different personality types, such as in the great tit system (van Oers et al. 2004a, b, c) thus gaining insight into the evolution of animal personalities (Fidler et al. 2007).

Despite the potential importance of determining a genetic basis to animal personality to our understanding of the evolution of personality, it remains problematic for most behavioural ecology researchers as it requires as a first step both large sample sizes and knowledge of pedigrees and relatedness to enable sampling across multiple generations which is often not possible or realistic in wild populations (Dochtermann 2011, Wilson et al. 2010). Additionally, due to the complex interactions of internal and external factors in shaping the phenotypes underpinned by genotypes, direct links

between genes and behaviour (such as those detailed above) are likely to be rare in the majority of systems.

Since gene expression is influenced by multiple factors experienced both early and later in life (Stamps and Groothuis 2010b, Groothuis and Trillmich 2011), early life experiences are thought to canalize personality traits by starting an individual on an ontogenetic trajectory that sets its later personality type (Sih et al. 2004b). These influences can occur prior to birth through both maternal and paternal effects encouraging correlations between genotypes and experiential factors that affect behavioural development (Stamps and Groothuis 2010b). For example, differing concentrations of steroid hormones deposited in eggs of great tits has profound effects on a variety of personality traits of the offspring hatching from those eggs (Groothuis et al. 2005). Furthermore, concentrations of hormones in eggs differ across lines of great tits artificially selected for different exploratory personality, suggesting that correlations between maternal genotypes and experiential factors that affect offspring personality begin early in the development of this species (Groothuis et al. 2008). These results reflect an organizational role of hormones whereby early developmental effects of hormones organize brain anatomy and neurochemistry, determine the distribution of hormone receptors, and act on aspects of morphology or physiology (Moore 1991, Dufty et al. 2002, Sih et al., 2004b, Duckworth and Sockman 2012).

Development experiences are not restricted to maternal and paternal effects, but also include physical and social environmental conditions (Dingemanse et al. 2009, Stamps and Groothuis 2010a, b). Experimental manipulations of early life conditions in Trinidadian guppies (*Poecilia reticulata*) showed that individuals from habitats with unpredictable food availability develop as bolder and more exploratory individuals than those from predictable habitats (Chapman et al. 2010). In addition, Bell and Sih (2007) showed that exposing juvenile three-spined sticklebacks (*Gasterosteus aculeatus*) to different predation pressures altered the correlations between personality traits. Early environmental experiences can thus influence both influence the development of personality traits, but also the presence and development of behavioural syndromes.

Although developmental conditions effectively ‘set’ the patterns of behaviour, personalities often remain somewhat malleable throughout life. Experiences later in life can serve to further reinforce personality traits, or conversely, serve to reshape or even dissolve previously correlated behaviours (Sih et al. 2004a, Stamps and Groothuis, 2010a, b, Groothuis and Trillmich 2011). The impact of experiential factors later in life are thought to be particularly influential in shaping personality traits when there is a major life history change such as dispersal, sexual maturation, or migration associated with the event (Stamps and Groothuis 2010b, Wilson and Krause 2012). For example, decisions such as where to settle and establish territories can influence nutrition intake and growth thereby influencing personality traits and differences between individuals (see Stamps 2007, Biro and Stamps 2008, Stamps and Groothuis 2010a, b). Hormones can influence the expression of personality traits through activational effects manifested later in life, such as when a hormonal surge elicits a specific behavioural response in a particular context (e.g. a surge in testosterone promoting fighting behaviour in a competitive encounter; Moore 1991, Sih et al. 2004b, Duckworth and Sockman 2012). Activational effects of hormones are a dynamic process through which the endocrine system can mediate an individual’s ability to behaviourally respond to social and environmental cues (Dufty et al. 2002, Duckworth and Sockman 2012). The influence that activational hormonal effects have on behavioural traits will depend on the hormone receptor system establish through organizational effects of hormones (Moore 1991, Dufty et al. 2002, Sih et al. 2004b, Ball and Balthazart 2008, Adkins-Regan 2012, Duckworth and Sockman 2012). An organizational effect can act to fix a male into certain social strategy (i.e. territorial or floater), and activational hormone effects can then trigger short term expression of type specific behaviour patterns (e.g. sedentary satellite behaviour versus wide-ranging mate search).

A number of recent studies have documented that individuals may have distinct physiological profiles (consistent, intra-individual differences in plasma hormone concentrations and/or metabolism), which, when combined with intra-individual differences in behaviour, suggests a pleiotropic influence on physiology and behaviours (Ball and Balthazart 2008, Kempnaers et al. 2008, Williams 2008, Réale et al. 2010b, Ouyang et al. 2011, Baugh et al. 2012, Careau and Garland 2012, Cook et al. 2012). Metabolic rates, personality and physiology are all likely to be

interrelated. Indeed, it may be argued that metabolic rate and personality are not causally linked, but rather share a correlation because of a common hormonal basis (Careau et al. 2008). For example, aggression is often positively associated with testosterone concentrations, and testosterone and metabolism are often linked, with higher testosterone increasing energy expenditure which results in a higher resting metabolic rate (see Gupta and Thapliyal 1985, Al-Sadoon et al. 1990, Wikelski et al. 1999, Olsson et al. 2000, Ros et al. 2004, Soma 2006, Careau and Garland 2012).

Correlations between physiological and behavioural traits have been termed the pace-of-life syndrome, and are thought to be the result of past selection pressures on the developmental stability and homeostasis of an organism, or correlational selection pressures associated with differences in fitness outcomes among the possible phenotypic combinations (McGlothlin and Ketterson 2008, Réale et al. 2010, Careau and Garland 2010, Réale et al. 2010b). While a number of recent reviews have called for increased attention to be focused not only on the relationship between consistent individual differences in metabolic rate and animal personality, but also on the interplay of hormones, metabolic rate and personality (Careau et al. 2008, Biro and Stamps 2008, Biro and Stamps 2010, Careau and Garland 2012), there has been little empirical research (Réale et al. 2010b). Understanding the degree of consistency in intra-individual differences in physiology, the extent to which this represents differences in underlying quality or differences in the environment (social and physical) and their relationship to behaviour and fitness can increase our understanding of evolutionary dynamics (Williams 2008, Ouyang et al. 2011). Examining the extent of consistent individual differences in hormones will also allow a better understanding of the role of the endocrine system in the organization and maintenance of personality, as understanding selection for personality traits can only be achieved through a comparable investigation of the mechanisms that regulate such traits (Sih et al. 2004b, Adkins-Regan 2005, Kempenaers et al. 2008, Williams 2008, Ouyang et al. 2011).

Proximate mechanisms are not isolated from each other. Genes, the environment, development, and their interaction influence neuroendocrine mechanisms which in turn influence suites of behaviour (see Figure 1; Dufty et al. 2002, Sih et al. 2004a, b, McGlothlin and Ketterson 2008, Stamps and Groothuis 2010a, b). Physiology is one

important link between the genome and the environment; the endocrine system in particular can interpret environmental variation to produce a range of phenotypes from the same genotype (Dufty et al. 2002). Furthermore, individual phenotypic responses will be influenced by experiential factors during development, so that conspecifics neither produce the same endocrine signals in response to specific environmental factors, nor do they respond in the same way to a given hormonal message (Dufty et al. 2002). Thus hormones, due to their universal nature resulting in simultaneous effects on multiple traits, have been proposed as a key mechanism that organizes, and maintains, behaviours in structured, correlated suites (i.e. personalities; Koolhaas et al. 1999, Baugh et al. 2012, Sih et al. 2004a, b). Gaining an understanding of this complicated and dynamic process between proximate mechanisms, and personality is key to our understanding of both the proximate basis, and ultimate outcomes, of personality.

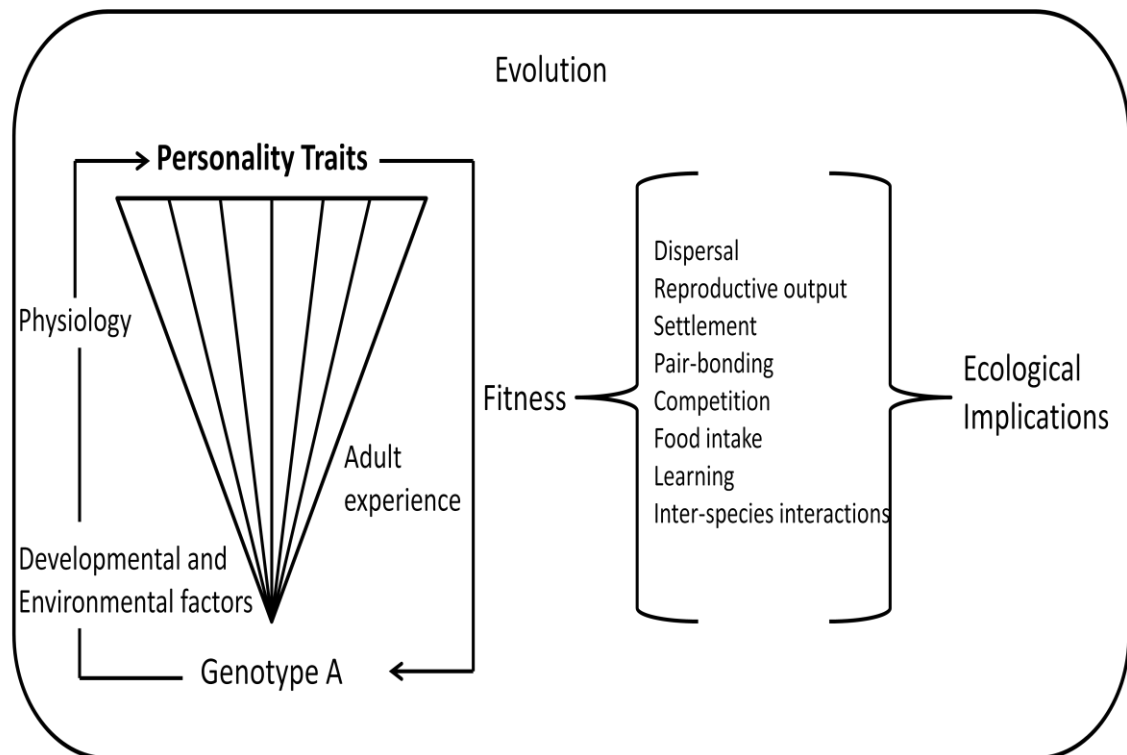


Figure 1: Conceptual diagram outlining the key sources of variability underlying the expression of animal personality traits and the ecological outcomes of personality, and the complex and dynamic nature of these interactions (adapted from Carere and Eens 2005).

Where to from here?

Despite recent interest in animal personalities prompting an explosion of empirical and conceptual studies (Wolf and Weissing 2012), with personality traits described for a range of taxa (see reviews by Gosling 2001, Sih et al. 2004a, b, Bell 2007a, b, Réale et al. 2007, Smith and Blumstein 2008, Bell et al. 2009, Réale et al. 2010a, Sih et al. 2012, Wolf and Weissing 2012), few studies have considered both the potential proximate causes of personality and the ecological outcomes of personality in a single species (but see the body of work on great tits, *Parus major*, which overall combines these two aspects: e.g. Dingemanse et al. 2003, Drent et al. 2004, Dingemanse et al. 2004, Carere and van Oers 2004, van Oers et al. 2004a, b, c, Both et al. 2005, Hollander et al. 2008, van Oers et al. 2008, van Overveld and Matthysen 2010, Amy et al. 2010, Baugh et al. 2012). This is perhaps in part due to the complicated and dynamic nature of the (likely) interactions between proximate mechanisms and ecological outcomes in shaping the structure, outcomes and evolution of personality.

One potential avenue is therefore to focus on a specific personality trait that is likely to be important in a given species, and investigate the proximate mechanisms and ultimate outcomes of that trait.

Aggression as a key axis of personality variation

One of the most frequently studied behavioural traits is aggression (Gosling and John 1999, Honess and Marin 2006, Réale et al. 2007, Freeman and Gosling 2010).

Aggression is important for a number of key fitness and population level parameters (Le Galliard et al. 2005, Mougeot et al. 2005, Duckworth 2006, Duckworth and Badyaev 2007, Fuxjager and Marler 2010, Kasumovic et al. 2010, Huang et al. 2011, Wilson et al. 2011). It has clear links to the endocrine system through its interaction with the sex steroid hormone testosterone (Moore 1991, Moore et al. 1998, Groothuis et al. 2005, Rhen and Crews 2002, Ryan and Vandenbergh 2002, Trainor et al. 2004, Oyegbile and Marler 2005, Adkins-Regan 2012), and has been demonstrated to have a heritable basis (Bakker 1986, Parmigiani et al. 1999, Alaux et al., 2009, Schumer et al. 2011). This makes aggression ideal as a key personality trait for studies of the fitness effects and potential evolutionary implications of animal personality.

Aggression is associated with a number of fitness related outcomes, most notably in intra-sexual male competition. Highly aggressive individuals (compared to conspecifics) are often better competitors for limited resources such as food, shelter and mates (Thompson and Moore 1991, Arnott and Elwood 2009, Herrel et al. 2009) and aggression has been shown to be associated with dominance and territory acquisition and defense (e.g. Beaugrand et al. 1991, Schulte-Hostedde and Millar 2002, Duckworth 2006, David et al. 2011). Increased access to resources often results in increased fitness through reproductive success. In western bluebirds (*Sialia mexicana*) for example, more aggressive males outcompete less aggressive males for high quality breeding habitat (more nest cavities) which results in greater reproductive success, and individuals that aggressively defend larger territories also enjoy access to greater food resources (Duckworth 2006). Aggression is also important to parental care, with more aggressive black-tailed gull (*Larus crassirostris*) parents more effectively protecting their nests, and thus suffering lower nest predation (see Kazama and Watanuki 2010).

Aggression can also influence dispersal (Duckworth 2006) and can be an important determinant of population level processes such as territory spacing, population density and population dynamics (Le Galliard et al. 2005, Mougeot et al. 2005, Duckworth 2006, Duckworth and Badyaev 2007). Mougeot et al. (2003, 2005) demonstrated that aggression in red grouse (*Lagopus lagopus scoticus*) regulates population density and influences population structure via affecting the kin structure of male populations and recruitment to territorial breeding grounds in both sexes, resulting in cyclic dynamics of red grouse populations. Le Galliard et al. (2005) demonstrated that male aggression in male-biased populations of common lizards (*Lacerta vivipara*) can threaten the viability of populations when aggression is directed at females. Increased male density resulted in increased sexual aggression against females whose survival, birth and emigration rates dropped. This can ultimately result in population collapse (Le Galliard et al. 2005). Finally aggression can also influence inter-species interactions and community dynamics. For example, Duckworth and Badyaev (2007) showed that highly aggressive male western bluebirds occurred at the invasion front as the species colonized new areas, resulting in the displacement of less aggressive mountain bluebirds (*Sialia currucoides*). This aggressive behaviour represents an adaptive strategy: once mountain bluebirds are displaced, aggression decreases in successive generations of western bluebirds (Duckworth and Badyaev 2007). Through its effect on population demographic processes and inter-species interactions, aggression can thus be an important determinant of the evolutionary trajectory of populations (Mougeot et al. 2003, Duckworth 2006, Duckworth and Badyaev 2007). For example, aggressive competition within western bluebirds populations results in the sorting of aggressive and non-aggressive males into distinct habitats. These habitats differ in the strength of selection on morphological traits (via foraging techniques) and demonstrate that aggression can affect selection on a local scale by influencing settlement patterns (Duckworth 2006).

The aggression personality trait is also an excellent model trait with which to study the potential proximate basis of personality. A number of studies involving selection experiments in a range of taxa have demonstrated that aggression has a strong heritable genetic component (Bakker 1986, Parmigiani et al. 1999), is a complex polygenetic trait (Alaux 2009) and that there is overlap between species in core sets

of genes related to aggression (Alaux et al. 2009, Schumer et al. 2011). However, aggression and environmental factors are also linked, with variation in social organization, age and experience all (potentially) inducing differences in aggression within or between species, even when the same genes coding for aggression are selected for (Alaux et al. 2009). While aggression can have a genetic basis, the expression of aggression is often controlled by complicated feedback loops associated with the endocrine system (Moore 1991, Moore et al. 1998, Groothuis et al. 2005, Rhen and Crews 2002, Ryan and Vandenberg 2002, Trainor et al. 2004, Oyegbile and Marler 2005, Adkins-Regan 2012). This represents an example of phenotypic expression of genotypes being influenced by physiological pathways established through development, and interacting with environmental factors.

Both the organizational and activational role of hormones (particularly testosterone) on aggression have been demonstrated. Experimental elevation of androgens in eggs in a number of bird species resulted in earlier hatching dates, increased mass at hatching and increased begging behaviour in chicks, subsequently resulting in earlier food provisioning from parents, increased growth and earlier fledging dates relative to siblings (see review by Groothuis et al. 2005). The activational relationship between testosterone and aggression has also been considered, with a number of studies demonstrating that circulating testosterone concentrations rise following an aggressive encounter and may act to sustain aggressive behaviour and enhance an individual's ability in future aggressive encounters (Trainor et al. 2004, Oyegbile and Marler 2005 and references in both). Similarly, artificially increasing circulating testosterone concentrations result in an increase in aggressive behaviour and enhanced an individual's ability to win a competitive interaction (Trainor et al. 2004). In male California mice (*Peromyscus californicus*), for example, testosterone levels rise naturally following an aggressive behaviour (Oyegbile and Marler 2005). Trainor et al. (2004) demonstrated that this increased testosterone resulted in males displaying more aggressive behaviours the following day, thus enhancing their ability to win future fights.

A study system in which to examine personality in a holistic manner must fulfill a number of requirements. The first of these is that the personality trait of interest will have important implications for individuals within a population. Secondly, the system

must be amenable to field-based research on an ecologically relevant timescale. As demonstrated through personality research on great tits for example (Dingemanse et al. 2003, Drent et al. 2004, Dingemanse et al. 2004, Carere and van Oers 2004, van Oers et al. 2004a, b, c, Both et al. 2005, Hollander et al. 2008, van Oers et al. 2008, van Overveld and Matthysen 2010, Amy et al. 2010, Baugh et al. 2012), it is only through long-term ecologically relevant field studies that both the proximate mechanisms and ecological outcomes of personality can be integrated into an evolutionary framework. Individuals in such a population therefore need to be easily caught and marked for field observations. Thirdly, system needs to be open to laboratory manipulation, including hormonal manipulation, as both establishing personality, and untangling the complex nature of personality-physiological interactions, will require experimental manipulations. Reptiles make an excellent model system which fulfills these requirements (for example, see work by De Nardo and Sinervo 1994, Whiting 1999, Sinervo et al. 2000, Stapley and Keogh 2004, Lopez et al. 2005, Stapley and Keogh 2005, Cote and Clobert 2007, Uller et al. 2007, Warner et al. 2007, While et al. 2009b, c, Wapstra et al. 2010). Additionally, aspects of the proximate mechanisms and ecological role of personality has begun to be established in some species (for example see work by Stapley and Keogh 2004, 2005, Cote and Clobert 2007, Sinn et al. 2008, While et al. 2009a, Rodriguez-Prieto et al. 2011).

This thesis is grounded in the extensive information that has been collected on a population of social lizard species, *Egernia whitii*. Crucially, consistent individual variation in aggression has previously been established in this species, and is known to be important to females in the population (see Sinn et al. 2008, While et al. 2009a) making this the ideal trait in this system with which to begin an investigation into the proximate causes, and ecological outcomes, of personality.

***Egernia whitii* – a model study system**

Egernia whitii is a medium sized viviparous lizard that lives in small family groups. Adult males and females form long-term pair bonds (pair-bonds are stable across seasons) and are largely monogamous, although there is approximately 25% extra-pair paternity (While et al., 2009c, e, 2011). Both adult males and females maintain long-term individual home-ranges (see While et al 2009c, e, 2011), with the adult pair

having an overlapping core area with a shared central burrow (or burrows). Offspring (first, second or third year) are tolerated within the home range and, although there is no direct parental care, tolerance of offspring potentially provides protection from infanticide (While et al. 2009a, e). Adult males discriminate between within-pair and extra-pair offspring, tolerating within-pair offspring and excluding extra-pair offspring from his home range (While et al. 2009c). There is considerable variation in the levels of social organization within populations of *Egernia* (reviewed in Chapple and Keogh 2005, 2006, While et al. 2009e). This variation in social organization has implications for male fitness, with both the sexual composition of a male's social group (monogamy vs. polygyny) and the acquisition of extra-pair paternity strongly influence variance in male reproductive success (While et al. 2011). Social organization is largely the result of competition over specific habitat characteristics (burrowing sites: Chapple 2003, and areas of high thermal quality: Langkilde et al. 2003), and environmental variation across territories could be the driving predictor of variation in social organization. A behavioural trait that influences social organization and acquisition of territories will therefore be highly important in this system and has the potential to have a large influence on the evolutionary trajectory of populations.

Consistent individual variation in aggression has previously been established in a population of *E. whitii* in Tasmania, Australia, and has been demonstrated to have important ecological implications. Both male and female *E. whitii* display consistent, long term (across season) individual differences in aggressive behaviour (Sinn et al. 2008, While et al. 2009a). Aggression in females influences aspects of their social organization, with increased female aggression strongly linked to increased rates of extra-pair paternity (While et al. 2009a). This imposes severe fitness costs in terms of reduced paternal care as males do not tolerate extra-pair offspring (While et al. 2009a). However, more aggressive females (relative to others in the population) also have higher clutch survival, suggesting that they are better care givers, thus offsetting the cost of reduced paternal care of the extra-pair young (Sinn et al. 2008, see also O'Connor and Shine 2004). While aggression in females has clear and important fitness implications, the ecological importance of aggression in males is not yet understood. Male aggression is potentially important in determining resource acquisition (territory size and quality) and thus influencing male fitness. The eco-evolutionary links between environment, aggression and aspects of social dynamics

(i.e. adult density, reproductive output, within- and extra-pair paternity) are also yet to be examined. Given what has already been established in this system relating to aggression, and the key features of a model system that apply to this species (see above) *Egernia whitii* represent an excellent model with which to address both the proximate basis of personality, and the ecological role of personality.

Research Objectives and Thesis structure

The overall aim of my thesis was to investigate the proximate basis and the ecological outcomes of personality in a free-living animal population. To achieve this, I based my research on a well-characterised population of the Australian social lizard species *Egernia whitii*. I first investigated the overall presence and structure of, and correlations between, five key personality traits in this population (using the definitions provided by Réale et al. 2007). Based on the results of this study, and previous work in this population (see Sinn et al. 2008 and While et al. 2009a), I then focused on investigating the proximate basis and ecological outcomes of the key personality trait aggression. I therefore had three main aims, as detailed below.

1. To examine the structural definition, presence of, and links between, five key personality traits (aggression, boldness, exploration, sociability and activity).

A number of personality traits have been identified within the animal personality literature, but there are five clear traits that relate to separate ecological conditions, and are potentially key targets of selection. These traits are (using the definitions in Réale et al. 2007): i) *shyness-boldness* which describes an individual's reaction to any risky, but not new, situation; ii) *exploration-avoidance* which describes an individual's reaction to a new situation; iii) *activity* which describes the general level of activity of an individual; iv) *aggressiveness* which describes an individual's agonistic reaction towards conspecifics; and v) *sociability* which describes an individual's reaction to the presence or absence of conspecifics (excluding aggressive behaviour). While some studies have considered several personality axes simultaneously (e.g. Weiss et al. 2000, Sinn and Moltschaniwskyj 2005, Weiss et al. 2006, Dingemanse et al. 2007, Moretz et al. 2007, Dingemanse et al. 2009b, David et al. 2011, Rodriguez-Prieto et al. 2011), studies involving multiple personality traits,

such as those outlined above, are still relatively uncommon, yet potentially very important. Links between these traits would indicate that the traits are not free to vary and evolve independently, but that changes in, or selection on, a trait in one situation could have important repercussions for linked traits important in other situations. Determining the links between these five traits will therefore be important in investigating the ecological and evolutionary implications of individual variation in these personality traits.

I determined the presence of the above five key personality traits in *E. whitii* (Chapter 2) by designing laboratory based behavioural tests to target the measurement of each of these traits. I also established the short-term structural consistency of these traits, and examined the correlations between these five personality traits.

2. To investigate testosterone as a potential proximate basis of personality, using aggression as a key personality trait, and to establish the potential physiological cost of aggression.

Hormones are typically regarded as a key link between the genome and the environment, and the variation in the environment is commonly interpreted behaviourally via the endocrine system. Given the extensive literature regarding links between the sex steroid hormone testosterone and aggression (see above) and the establishment of aggression as a key personality trait in *E. whitii* (Sinn et al. 2008, While et al. 2009a), the logical approach to examine a potential proximate basis to personality is to investigate the role of testosterone in maintaining and activating aggression in this species. As such, I/we established the links between circulating baseline concentrations of testosterone and consistent individual differences in aggression in both male and female *E. whitii* in a field-based study (Chapter 3: While et al. 2010). I then investigated the activational relationship between testosterone and aggression by conducting a complementary two-part laboratory based experiment in which I both experimentally manipulated testosterone concentrations, and subjected lizards to a behavioural challenge, in order to understand if, and how, testosterone influenced or was influenced by, aggression in this species (Chapter 4).

In order for a personality trait to be maintained within population, there should be both costs and benefits associated with that trait (see above). One potential cost of aggression is oxidative stress. Aggression is often regulated by steroids (see above) which can influence oxidative metabolism and increase whole body metabolic rate and physical activity independently of aggression (e.g., Gupta and Thapliyal 1985, Al-Sadoon et al. 1990, Wikelski et al. 1999, Olsson et al. 2000, Ros et al. 2004, Soma 2006). Therefore, if aggression comes with a physiological cost, understanding the links between an individual's inherent level of aggressiveness, its mediating hormones (e.g., testosterone) and oxidative stress will be crucial for fully understanding the consequences of personality traits and how interspecific variation in behaviour is maintained (Isaksson et al., 2011a). I/we therefore examine the links between aggression, circulating testosterone and oxidative stress parameters in a *E. whitii*. Specifically, we examine three oxidative stress parameters, measured in blood plasma, including antioxidant capacity (OXY), reactive oxygen metabolites (ROMs) and an estimated oxidative stress index (OI) based on the proportion of ROM to OXY (Vassalle, 2008) (Chapter 5: Isaksson et al. 2011b).

3. To investigate the ecological role of aggression as a key personality trait in *Egernia whitii*.

Previous research in *E. whitii* has shown that consistent intra-individual aggression in females is important in terms of mating opportunity, with more aggressive females sourcing more extra-pair mating opportunities (see While et al., 2009a). Individual aggression in females is also important for offspring survival with offspring born to more aggressive females having a higher probability of survival (see Sinn et al., 2008). However, the importance of aggression to males in this system is not yet understood. Aggression is typically important in agonistic interactions between males, with the more aggressive individuals often achieving a successful competition outcome. Within the *Egernia* system, anecdotal evidence suggests that variance in habitat quality (substrate available for crevice construction) is the primary driver of variance in male acquisition of females and thus the key resource over which individuals compete (see discussion in While et al. 2009b, While et al. 2011). I integrated a detailed field study on the effects of aggression on home range size, overlap and male reproductive success, factors which are likely outcomes of

competitive interactions in the wild, with a laboratory manipulation of resource availability (i.e. basking sites) to determine the potential ecological outcomes of aggression in male *E. whitii* (Chapter 6: McEvoy et al. 2013).

Individual variation in behaviour is important for intra- and interspecific interactions and influences ecological networks which can result in evolutionary change (Wolf and Weissing 2012). Aggression is both influenced by, and influences, an individual's physical environment and individual differences in aggression have strong and persistent effects on fitness-related traits linked to social strategies. Environmental variation is likely to influence population demographic process such as density, and both density and environmental variation will interlink with aggression. This interplay is likely to subsequently influence social organization and population demographics. I conducted a detailed field study to investigate the interplay of aggression, environment and density in determining reproductive output for both male and female *E. whitii* (Chapter 7).

Thesis Presentation

This thesis comprises six data chapters (and one appendix) designed to assess the aims outlined above. Three of these chapters have been accepted for publication in relevant journals (Chapter 3, Chapter 5, Chapter 6). The remaining three data chapters are either in review or in preparation for submission at relevant journals and all have thus been written as stand-alone pieces of work. When fitted into the context of the thesis, these chapters provide the appropriate information to address the overall objectives of this study. Due to the nature of this thesis, each chapter may incur some repetition, particularly in terms of animal collection and species description. Each chapter may vary with respect to formatting, as each has been formatted according to the specifications of the journal to which it was submitted (or will be submitted). This project utilized a multidisciplinary approach, and I take intellectual carriage for the overall thesis presentation and contents, as reflected in senior (1st) authorship on 4 of the 6 presented papers. However, given the multidisciplinary design of this thesis, and the collaborative nature of the *Egernia* system, there are two data chapters which were driven by and benefitted from substantial contributions by collaborators. As they were crucial in the context of addressing the aims of this study, and I made substantial contributions to the conceptual basis and execution of these studies (and

resultant publications), they have been included. In addition, the large-scale, integrated nature of this study resulted in the collection of data on parameters that do not fit directly into the context of this thesis. Papers stemming from these data are either included here as an appendix or are still in preparation and will be submitted for publication at a later date.

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Chapter Two

An examination of personality in a social lizard species, *Egernia whitii*: testing the structure of, and correlation between, five key personality traits

Abstract

Personality can be thought of as an individual's aggregated summary trend in behavior, capturing characteristic patterns of behavior that persist across time. Animal personality is ubiquitous throughout the animal kingdom and has important implications for individual fitness. Animal personalities also help to explain apparently mal-adaptive or sub-optimal behavior when personality traits are correlated across contexts. While a number of personality traits have been identified, there are perhaps five key traits that have been used to describe animal personality (aggression, boldness, exploration, activity and sociability) and are potentially key targets of selection. We measured these five personality traits in a native Australian social skink species, *Egernia whitii*, paying particular consideration to consistency in the structural definition of the personality traits, intra-individual consistency in the traits, and the correlations between personality traits. We found that at the level of personality trait structure, relationships between observed behavioral variables within each trait were fluid and differed depending on sex and time. The only personality trait that had a consistent structural definition was aggression. We found variability in the short-term consistency of traits, with strong consistency in aggression, moderate consistency in exploration, boldness and activity and a lack of consistency in sociability. Finally, we found that correlations among different personality traits (i.e., behavioral syndromes) were also time- and sex- specific. We discuss the relevance of structural consistency and intra-individual consistency of traits to inter-trait correlations, and overall suggest that care should be taken when attempting to characterize personality traits.

Introduction

Animal personality captures an individual's characteristic patterns of behavior that persist across time and situations (Buss and Craik 1983; Gosling 1998). For example, an individual that is relatively more aggressive than conspecifics at a particular point in time, will also be relatively more aggressive at another point in time, or an individual that is more exploratory in novel environments will also tend to be more willing to approach novel objects in known environments. Recent studies have shown that animal personality appears to be ubiquitous throughout the animal kingdom (Gosling 2001; Sih et al. 2004a, b; Sih and Bell 2008; Bell et al. 2009). Personality can have important implications for individual fitness (e.g., Smith and Blumstein 2008) and as a result, can influence population dynamics and selection through its effects on group composition (e.g. Flack et al. 2006; Krause et al. 2010), natal dispersal (e.g. Cote et al. 2010), social learning (e.g. Reader 2003), cooperation (e.g. Bergmuller and Taborsky 2010), pair bonding (e.g. Dall 2004; While et al. 2009a), parental care (e.g. Sinn et al. 2008b) and disease and parasite spread (e.g. Capitanio et al. 1999; Barber and Dingemanse 2010). The idea of consistent individual differences in behavior, while not new, has increasingly become a key target of research (Bell 2007; Sih and Bell 2008; Dall et al. 2012).

A number of personality traits have been identified within the animal personality literature, but there are perhaps five most commonly examined traits that are potentially key targets of selection. These traits are (using the definitions in Réale et al. 2007): i) *boldness* which describes an individual's reaction to any risky, but not new, situation; ii) *exploration* which describes an individual's reaction to a new situation; iii) *activity* which describes the general level of activity of an individual; iv) *aggressiveness* which describes an individual's agonistic reaction towards conspecifics; and v) *sociability* which describes an individual's reaction to the presence or absence of conspecifics (excluding aggressive behavior). Links between these traits would indicate that the traits are not free to vary and evolve independently, but that changes in, or selection on, a trait in one situation could have repercussions for linked traits important in other situations (Dall et al. 2004; Sih et al. 2004a, b; Pruitt et al. 2008; Sih et al. 2012). Determining the links between these five traits is therefore important for studies investigating the ecological and evolutionary implications of individual variation in these traits. Although a number of studies have

considered multiple personality traits simultaneously (e.g. Weiss et al. 2000; Sinn and Moltchanowskyj 2005; Weiss et al. 2006; Dingemanse et al. 2007; Moretz et al. 2007; Dingemanse et al. 2009; Wilson et al. 2010; David et al. 2011; Rodriguez-Prieto et al. 2011), few studies have considered the five key traits outlined above in an un-manipulated wild population.

We aimed to measure these five personality traits in a free-living vertebrate population, paying particular attention to the nature of the personality traits. In order to measure a personality trait, we first ideally need to determine if the structural consistency of the traits (i.e. the behavioral definition of the trait) is the same across the measurement or observation period (Caspi and Roberts 1999; Stamps and Groothuis 2010). Since animal personality traits are generally (but not always) quantified as an aggregate measure of observed behaviors (Gosling 1998), the ‘definition’ of an aggregate personality trait (i.e., the relationships amongst the observed behaviors which contribute to aggregate scores), should remain consistent through time to form a functionally coherent category (Gosling 1998; Dingemanse et al. 2010). Secondly, it is important to establish the extent of intra-individual consistency for a given personality trait through time. This is particularly important in studies that propose to measure multiple, separate aggregate personality traits, as consistency of traits can influence correlations between traits (Stamps and Groothuis 2010). Once structural consistency and intra-individual consistency is established one can begin to examine covariance between traits and explore the functional significance of single traits as well as correlations between traits (i.e. behavioral syndromes).

To achieve our goal of measuring the aforementioned five personality traits in a free-living vertebrate, we integrated a number of key sub aims that explicitly addressed the potential issues identified above. Specifically, we aimed to 1) establish the structural consistency of each of our personality traits at two time points, 2) examine the extent of intra-individual consistency within each of the personality traits, and 3) examine the inter-correlations between personality traits. Combined, this approach allows us to ascertain the nature of personality in a wild population of vertebrates, and in general, provides an example of an in-depth characterization of multiple personality traits in a nonhuman animal species.

Methods

Study Species

White's skink (*Egernia whitii*) is a medium sized (up to 100mm snout-vent length, SVL) viviparous skink found throughout a broad range in southeastern Australia. We used *E. whitii* from a population on the east coast of Tasmania, Australia (42°57' S, 147°88' E). Individuals at the study site are found in discrete patches of open grassland in close proximity to excavated burrows or rock crevices that they use as retreat sites. Males and females become reproductively mature at approximately 3 years and have an overall lifespan of 9-10 years (While et al. 2007). Recent research has shown that the social organization of Tasmanian populations of *E. whitii* is based on small family groups composed of monogamous male/female pair bonds, with stable home ranges and some conspecific home range overlap (While et al. 2009b, c).

Field Protocol: Experimental individuals

We captured a total of 52 (31 males and 21 females) adult *E. whitii* in January - March 2009. Lizards were captured using mealworm fishing or noosing techniques, after which they were transported back to the specifically designed Terrestrial Ecology facilities at the University of Tasmania, where they were housed individually in plastic terraria (30 x 60 x 40 cm) in a room maintained at an ambient temperature of 16°C. Each terrarium was supplied with a basking light on an 8:16 hr light/dark cycle, and overhead lights on a 10:14hr light/dark cycle. Each terrarium had a basking rock under a light at one end, and a shelter at the opposite end (maintained at 15 cm from the closest edge of the basking rock) with water and food (mealworms (*Tenebrio* larvae) or pureed fruit with protein powder or Reptavite) available *ad libitum*. Once in the laboratory, all individuals were weighed and measured (snout-vent length, head width, head length, total length). Individuals in this study are part of a long-term life history study (While et al. 2007; 2009a, b, c; 2010; 2011; McEvoy et al. 2013) and as a result had previously been given individual toe-clips, allowing for unambiguous identification of all individuals.

Personality Trait Assays

We conducted a series of five laboratory based behavioral assays designed to specifically target each personality trait (as defined in Réale et al. 2007) with specific reference to *Egernia* ecology. All assays were conducted twice in a 12-day period to

allow for examination of within-individual consistency and between-individual variability (Fleeson 2004). No individual received the same assay in the same order (see Dochtermann 2010), no assay was conducted on consecutive days, and the order of assays each day was randomized. There was a minimum of two days between the first assay and second assay of each personality trait. All assays were conducted by a single experimenter (JM).

Conspecific Aggression Assay: Conspecific aggression testing followed the procedures outlined in Sinn et al. (2008a), While et al. (2009a; 2010), Isaksson et al. (2011) and McEvoy et al. (2013) for the same species. Briefly, individuals were given the aggression assays in their home terrarium. Home terraria had opaque sides that allowed for testing only one lizard at a time. Behavioral assays were run in the afternoon between 1400 and 1700 so that lizards could obtain their preferred body temperature (Stapley 2006).

Conspecific aggression assays consisted of the experimenter approaching the front of the home terraria and touching the lizard with a realistic soft plasticine model of an *E. whiti* attached at the end of a wooden dowel. Lizards were presented with the model after a 60 second acclimation period to the presence of the observer, but only if they were found and remained on the basking rock during the acclimation period. Subjects were touched up to 10 times on the snout by the model or until they fled into or on top of the shelter. We used an act-frequency approach to measuring behaviors in aggression assays (Martin and Bateson 1993; Sinn and Molschaniwskyj 2005). Four behavioral variables were measured: number of touches before the lizard fled (to a maximum of 10 touches); number of back arches (a display whereby the spine of the lizard was bent to form a concave arch); the number of times the lizard displayed with an open mouth; and the number of times the subject actively bit the model. These behavioral variables closely resemble those recorded in antagonistic interactions within this and other *Egernia* species (e.g. Langkilde and Shine 2004; O'Connor and Shine 2004; Langkilde and Shine 2005; Langkilde et al. 2005; Langkilde and Shine 2007; McEvoy et al. 2013) and have been observed in the wild by both GMW and JM. Behavioral variables in assays were recorded for the entire duration of stimulus presentation with an audiocassette recorder and hand held timer.

Variables were scored as a multiple frequency only if the lizard performed that behavior anew after each touch with the model.

Boldness Assay: As with aggression assays, individuals were given behavioral assays in their home terrarium and behavioral assays were run in the afternoon between 1400 and 1700. Boldness assays consisted of the experimenter approaching the front of the home terrarium and determining if the individual was basking. If the lizard was basking, it was immediately presented with a life-sized model (taxidermy specimen) of a kookaburra, a known predatory bird of this species (GW and JM pers obs). Model kookaburras with wings outstretched were presented by simulating a swooping action of the bird into the home terraria of the lizard. Model kookaburras were on a metal bar and pulley system so that the experimenter (JM) could swoop the kookaburra into the individuals cage without being observed by the lizard. Our primary interest was in the time taken for an individual to re-emerge from its shelter following the stimulated attack (e.g., Bell and Stamps 2004; Bell and Sih 2007). Kookaburras were therefore presented until the lizard fled. We recorded the number of simulated attacks taken before the lizard fled and then recorded time to re-emerge from the shelter following the attack. If, after a maximum of five minutes after fleeing individuals had not re-emerged, they received the maximum re-emergence time of 300 seconds (average time to re-emerge = 214 ± 117 seconds). None of the individuals displayed the behaviors observed in aggression assays (i.e. back arch or mouth open).

Exploration Assay: Exploration assays were conducted in a novel test arena (60cm x 80cm x 40cm) with novel objects present. In each arena we randomly placed four objects that lizards were unlikely to have encountered before; objects included a rubber ball that lit up with motion (which lizards could activate if they physically tried to climb the ball), plastic building blocks of various sizes, plastic foliage (as used in fish tanks), and spongy squeeze balls as well as different substrate including carpet, fake turf and smooth varnished plywood. As exploration is designed to capture individuals' reaction to novel objects/habitat (Réale et al. 2007; Rodriguez-Prieto et al. 2011), objects within test arenas were different for each assay the individual received. Activity in reptiles is tightly linked to body temperature (Hertz et al. 1982; Cooper 2000; Herrel et al. 2007), so assays were conducted after lizards had

access to a minimum of three hours of basking opportunity to achieve preferred body temperature (Stapley 2006). Individuals were transported from home terraria to the test arena in opaque plastic containers and allowed to acclimate for two minutes. Individuals were then removed from the transport container and allowed to explore the test arena for 30 minutes. In assay one, all but one individual explored the arena, in assay two, all individuals explored. Assays were videotaped with a DSP colour 1/3 inch security camera linked to a digital video recorder (Ganz DR16NRT DVR system). We recorded the latency to begin exploring the arena (the shortest latency to touch any of the objects) and the number of times individuals approached each object (approach was defined as touching the object with snout). We then calculated the total number of times the individual approached all objects (e.g., van Oers et al. 2004). Test arena and all objects were thoroughly cleaned with ethanol after each exploration test.

Activity Assay: Activity assays consisted of recording an individuals' behavior in their home cage at half hour intervals from 8am to 6pm (when the overhead lights were on, and one hour before and after the basking lights were on). The experimenter (JM) observed each individual lizard (without being seen by individuals) and recorded activity. Observations consisted of scanning each cage twice within a 10 minute interval at the beginning of each half hour. Behaviors recorded were: a = basking on rock, b = under shelter, c = moving around terraria, d = half under shelter, e = other (i.e., eating, elsewhere in cage, not on rock) (see Melville and Swain 1997 for similar classification). We were interested in 'active' behaviors and as such did not include basking behavior (behavior 'a') in our final activity behavioral score as this is a physiological requirement and is necessary before lizards can engage in any other activity. We also did not include the time an individual spent in the shelter (behavior 'b') as an active behavior as we could not observe whether individuals were active or not while in the shelter (i.e. individuals could potentially be burrowing under the shelter, or could be sleeping).

Sociability Assay: Sociability assays were conducted in the same test arena as exploration assays, but with a different interior design (see for example Cote and Clobert (2007) for sociability assays with juvenile lizards). For sociability, we were primarily interested in the propensity to socialize with unrelated conspecifics. Two

basking platforms were set up at either end of the test arena. At one platform the basking rock was sitting on top of a dish of clean paper pellets (i.e. no scent), at the opposite end the basking rock was sitting on top of scented paper pellets. Scented paper pellets were collected from a random assortment of terraria that had housed male and female adult *Egernia* from different experiments. These lizards had been collected from a different field site (> 1 km away) so familial relationships with the test subjects were unlikely. Individuals were denied basking opportunity for a half hour prior to the start of assay to provide incentive to choose a basking platform. Individuals were transported from their home terraria to the test arena in an opaque plastic container, were released into the centre of the test arena (which was partitioned off from rest of test arena with removable slides) and allowed two minutes to acclimate. Slides were removed and individuals were allowed 30 minutes to explore and bask. Assays were videotaped with a DSP colour 1/3 inch security camera linked to a digital video recorder (Ganz DR16NRT DVR system). We recorded the time spent basking on each platform. Test arenas and basking platforms were thoroughly cleaned with ethanol after each assay, and paper pellets (both clean and scented) were replaced after each assay.

Statistical Analysis

Behavioral score creation

Each of the five behavioral assays were performed twice, so for each assay at each time point we also created an individual score representative of that assay (10 unique scores total per individual). Differences in personality trait expression (i.e. the aggregate behavior scores) and the observed behaviors that defined each personality trait (i.e. the structural definition of traits) were analyzed separately with respect to sex. Sample sizes may differ slightly for some tests/comparisons as not all traits could be measured for all individuals.

Conspecific aggression: We subjected the four observed behavioral variables to principal components analysis (Tabachnick and Fidell 1996). In all cases the number of components chosen was based on eigenvalues > 1, a scree plot, the amount of variation in each factor, and interpretability (Cattell 1966; Zwick and Velicer 1986; Budaev 2010). For both males and females and at each time point (i.e., assay 1 or assay 2), the four behavioral variables were highly intercorrelated and loaded strongly

on a single component which explained $> 59\%$ of the variation (Table 1; see also Sinn et al. 2008a; While et al. 2009a; 2010; Isaksson et al. 2011 and McEvoy et al. 2013). Both the Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy and the Bartlett's test of sphericity indicated that the matrices used in analyses were suitable for PCA (Budaev 2010). For each individual at each assay time, we computed a single unit-weighted aggregate score using all four observed behavioral variables, which we call 'aggression'.

Boldness: We conducted Spearman's rho correlations to check for inter-correlation between the two observed behavioral variables for each sex at each time point (univariate distributions of both re-emergence time and number of attacks at both time points were not normally distributed and not conducive to transformation). While there were significant correlations between the two variables for males at time one, no significant correlations existed at time two for males or for females at either time one or time two (Table 2). Given the fluctuating relationship between the two observed variables across assay periods, and that we were primarily interested in an individual's response following a threatening situation and not necessarily its response during an attack itself, we used the standardized time to re-emergence for each individual to represent a bold score.

Exploration: We were interested in an individual's latency to explore the test arena and how thoroughly the individual explored (total number of approaches to all objects). As with the bold behaviors we checked for inter-correlation between these two behavioral variables using Spearman's rho (exploration variables were not normally distributed and not conducive to transformation). We found that for both males and females there was a significant correlation between the two variables at time one, however, this relationship did not exist at time two for either of the sexes. Due to this lack of consistent inter-correlation between the variables at the two time points, and in order to reduce the number of comparisons between traits, we therefore used only the standardized variable 'total number of approaches to objects' as a representation of 'exploration'.

Activity: Scores were calculated as proportion measures. Individual proportions were calculated over the whole day observation period (see above). As we were not interested in non-active behaviors (see above) we created a proportion measure of ‘active’ behaviors (‘c’, ‘d’, and ‘e’) relative to the total time over which we conducted measurements.

Sociability: Sociability was calculated as the standardized ratio of time spent basking in the scented versus unscented basking platforms (see above). In assay one, 36% of the lizards sampled both basking platforms, 17% sampled neither, 13% only basked on the scented platform and 32% basked on the unscented platform. In the second test, 59% of lizards sampled both platforms, 19% sampled neither, 4% sampled only the scented platform and 17% sampled only the unscented. However, in neither assay did any individual spend the entire 30 minutes basking; all lizards spent some of the time exploring the test arena.

Standardized scores for each assay were used in order to avoid spurious correlations arising from comparisons between scores measured on different scales (Field 2009). Standardization removes differences between scores in mean and variance with maintaining patterns of covariance (Dingemanse et al. 2010). As body size can affect the expression of personality traits in lizards (Lopez et al. 2005) we checked for correlations between personality trait scores and body size (snout-vent length and head width and length). We used Spearman’s rho correlations as the majority of scores were distributed non-normally and were not conducive to transformation. To examine correlations between personality trait scores and size we pooled scores across time points within an assay (e.g. average of aggression one plus aggression two; Epstein 1983) but we analyzed sexes separately. Although we conducted a large number of correlations, and thus increase our Type 1 Error rates, employing a correction procedure such as Bonferroni or the false discovery rate can increase Type II errors, and obscure small, but biologically significant, results (Garamszegi 2006). As suggested by Nakagawa (2004) and supported by Garamszegi (2006) we report r ’s and associated confidence intervals (see Figure 1), this also allows potential meta-analysis and comparisons across and between data sets.

Table 1. Solution matrix from principal components analysis for the four observed behaviors measured in *E. whitii* during in conspecific aggression assays.

Behavioral Trait	Behavior	Males, Time One	Males, Time Two	Females, Time One	Females, Time Two
Aggression	Touch	0.89	0.85	0.73	0.84
	Arch	0.96	0.93	0.85	0.86
	Open	0.81	0.88	0.92	0.94
	Bite	0.71	0.73	0.51	0.73
% Variation explained		72	72	59	72
KMO		0.63	0.72	0.45	0.63
Bartlett's		$\chi^2 = 84.10$; df = 6; p = 0.001	$\chi^2 = 71.65$; df = 6; p = 0.001	$\chi^2 = 32.86$; df = 6; p = 0.001	$\chi^2 = 39.19$; df = 6; p = 0.001

Table 2. Spearman's rho correlations between the two observed behavioral variables measured in *E. whiii* in the boldness assay and the exploration assay. * indicates significant correlations.

Trait	Behavioral Variables	Males, Time One			Males, Time Two			Females, Time One			Females, Time Two		
		n	r	p	n	r	p	n	r	p	n	r	p
Boldness	Emerge time & # attacks	30	0.52	< 0.01*	28	0.03	0.85	18	0.10	0.68	20	0.24	0.30
Exploration	Explat & total approaches	31	0.59	< 0.01*	31	0.25	0.16	21	0.61	< 0.01*	21	0.23	0.31

Consistency in personality traits

We used Spearman's rho to examine rank-order consistency of individuals in their personality trait score through time. We first ran models for each sex separately to check for significant differences in consistency between the sexes. Sex-specific differences were determined by graphically comparing confidence intervals (Cumming et al. 2007) and statistically using Fisher's Z statistic (Zar 1984). There were no sex-specific differences in consistency through time for any of the five personality trait scores (all Z's < 1.24, all p's > 0.116); therefore we re-ran our consistency estimates while pooling our data across the sexes. We also used confidence intervals and Fisher's Z to determine if consistency estimates between personality trait scores were different from one another (for example if aggression was more consistent than activity).

Correlations between personality traits (i.e. behavioral syndromes)

Within each time point (assay one or assay two), we used Spearman's rho to estimate correlations between personality trait scores (e.g., between aggression and exploration, a behavioral syndrome) for each sex. Where we found significant differences between the sexes in correlations between the personality trait scores we report results for each sex independently. Where our analysis indicated that personality trait correlations were similar across the sexes, we re-ran analyses pooling our data across the sexes. Differences in rho's representing behavioral syndromes were also tested using graphical comparisons of confidence intervals and statistically using Fisher's z tests.

All data was analyzed using IBM SPSS Statistics version 19.0.

Results

For both males and females, head width and head length were correlated (males: $r = -0.83$, $p = 0.0001$, $n = 31$; females: $r = -0.77$, $p = 0.0001$, $n = 21$) so we created a single unit-weighted aggregate score representative of 'head size' and used this in further analysis. For both sexes, neither snout-vent length nor the head size score correlated with any of the observed behavioral measures, or with any of the five personality trait scores (all r 's < 0.35, all p 's > 0.23).

Consistency of personality trait scores through time

There were no sex-specific patterns in Spearman's rank estimates through time for any of the personality trait scores. Across both sexes, there was strong maintenance of rank-order expression of aggression through time ($r_{46} = 0.67$, $p < 0.01$), while moderate but significant correlations of personality trait scores through time were observed for boldness ($r_{46} = 0.31$, $p = 0.031$), activity ($r_{52} = 0.29$, $p = 0.034$) and exploration ($r_{52} = 0.30$, $p = 0.026$). In contrast, the estimate for consistency in individual sociability scores was not different from zero ($r_{52} = 0.10$, $p = 0.441$).

Using graphical comparisons of the confidence intervals (see Figure 1) aggression was more consistent than any of the other traits. We used the Fisher Z statistic to confirm that the rho for aggression was statistically different to that for exploration ($Z = 2.27$, $p = 0.023$). As the confidence intervals between these two traits overlapped the most (see Figure 1), a statistical difference between these two traits indicated that aggression was also statistically different from all other traits. Similarly we used this method to determine if the consistency of sociability was statistically different from that of the other traits besides aggression, which it was not (all Z 's < -0.96 , all p 's = 0.3371).

Correlations between personality traits

At assay time one there was a significant negative relationship between aggression and sociability for females ($r_{19} = -0.58$, $p = 0.008$, $L95\%CI = -0.81$, $U95\%CI = -0.21$), but not at assay time two ($r_{17} = -0.28$, $p = 0.268$, $L95\%CI = -0.71$, $U95\%CI = 0.22$). Correlations between aggression and sociability for males were not different from zero at either time point (both r 's < 0.33 , p 's > 0.06 , $N = 31$ for males at assay time one and 30 for males at assay time two). The correlation between aggression and sociability in females at assay time one was not significantly different from this same correlation in females at assay time two ($Z = -1.02$, $p = 0.153$), however, it was significantly different from males at both time points (time one: $Z = -3.23$, $p = 0.0012$; time two: $Z = -2.57$, $p = 0.012$). There were no sex-specific differences in any of the other personality trait correlations at either time. Across all individuals, there was a negative relationship between activity and exploration at time one ($r_{52} = -0.30$,

$p = 0.028$ L95%CI = -0.46, U95%CI = -0.04), but not at time two ($r_{52} = -0.13$, $p = 0.351$ L95%CI = -0.30, U95%CI = -0.23); however, correlation coefficients between activity and exploration were not different from one another across the two test times ($Z = -0.90$, $p = 0.3681$). There were no other correlations between personality axis scores either at time one or time two (all r 's < 0.24, p 's > 0.100).

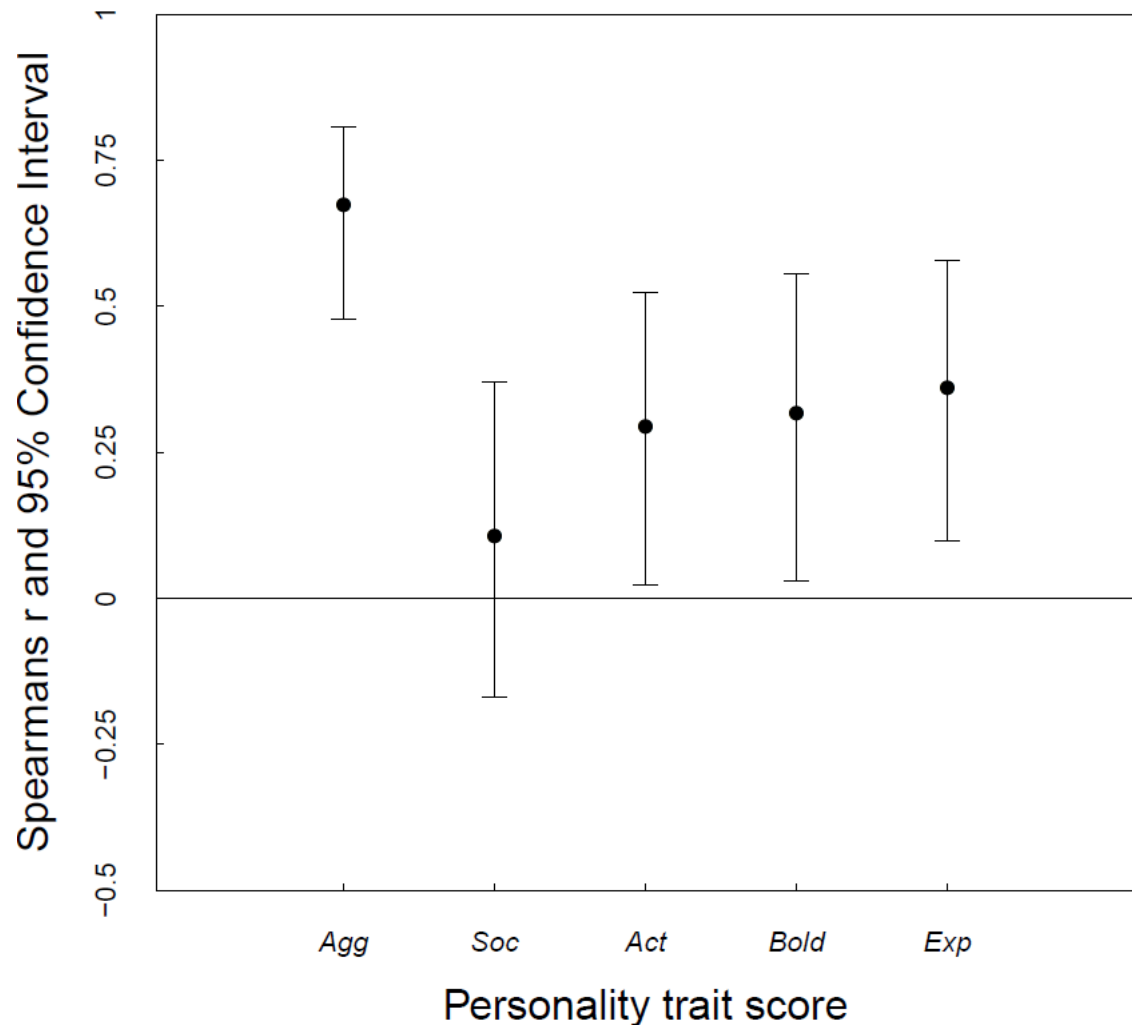


Figure 1: Plot showing the r_s and lower and upper 95% confidence intervals for each of the time one - time two correlations for personality axis scores for adult *E. whitii*. * indicates r_s is significant at the $\alpha = 0.05$ level. 'Agg' = aggression, 'Soc' = sociability, 'Act' = activity, 'Bold' = boldness, 'Exp' = exploration

Discussion

While the field of animal personality research has been steadily gaining interest over the last decade, few studies have taken an in-depth approach to examining the structure of multiple, commonly observed personality traits within the same population of animals. Here, in a wild population of *Egernia whitii*, we were able to design assays and measure behaviors in five main personality domains (Réale et al. 2007). However, we found that the structural consistency of personality traits and correlations both within and between personality traits were variable across both time and sex (see also Bell et al. 2009). Below, we discuss each of our results in turn and provide explanations for our findings. Overall we suggest that characterizing personality in nonhuman animals is not a trivial matter, and issues such as structural and temporal consistency should be taken into account prior to estimating across-context correlations (i.e., behavioral syndromes).

We found that the nature of the relationship between the behavioral variables that defined the *Egernia* personality traits changed over time in a sex-specific way. For example, in the boldness assay, the two observed behavioral variables ‘number of attacks’ and ‘time to emerge’ were positively correlated for males during the first assay (individuals that remained on a basking rock after a simulated predator attack also tended to re-emerge faster after eventually fleeing), but these same two observed behavioral variables were uncorrelated for males during the second assay, and were uncorrelated for females at both time points. Similar temporal patterns emerged for the two observed behaviors measured in the exploration assay. The fact that we found inconsistencies in the relationships between the behavioral variables within each test assay indicates that even at the most fundamental level (i.e. the relationship between observed variables), characterizing personality traits may be problematic.

Additionally, in our population of lizards the personality trait aggression was best characterized by a consistent aggregate behavioral score, while other traits (exploration and boldness) were best characterized by a singular behavioral variable. Again, our results indicate that relationships among variables that form a personality trait require examination to ensure that observed variables in any behavioral assay are consistently related to one another through time or across sexes prior to the construction of aggregate measures representative of an individual’s personality. Use

of aggregate scales that are constructed from observations across single time periods or collapsed across the sexes may result in the creation of unreliable personality trait scores, and subsequent analyses using these scores could result in spurious biological conclusions (John and Soto 2007). In short, structural consistency should be tested, not assumed.

One explanation for variable structural consistency among observed behavioral variables in some traits (boldness and exploration), but not others (aggression) is state-dependence (see Dingemanse and Wolf 2010; Luttbeg and Sih 2010; Wolf and Weissing 2010). State in this context refers to those features that are strategically relevant, including internal conditions (i.e. hunger, motivational state, size, age), external conditions (i.e. environmental conditions) and genes (i.e. the same phenotypic trait may be influenced by different sets of genes at different ages; see Martin and Réale 2008; Bell et al. 2009; Dingemanse and Wolf 2010; Wolf and Weissing 2010). In this scenario, if state-dependence played a large role in some observed behaviors (but not others), our laboratory assays may have been affected. For example, predation pressure often affects boldness, and factors that influence predation risk (such as size and energy reserves) will therefore influence individual differences in boldness (Luttbeg and Sih 2010). We attempted to control for the majority of these state-dependent factors (e.g. hunger, size and age: only adult individuals were captured, and seasonal effects were eliminated due to running the experiment in one season). However, the state-dependence of our observed behaviors is unknown. It is worth considering that the inter-relationships of behavioral variables is perhaps a fluid and dynamic phenomenon, and warrants further examination when defining the structure of personality traits.

One of the key premises of a personality trait is that inter-individual differences in the expression of the trait remain consistent over time. We found strong rank-order consistency in the expression of aggression, moderate consistency in the expression of boldness, activity, and exploration and weak-to-no consistency in sociability. There were no sex-specific differences in the consistency of personality traits. One explanation for these results is that individuals became habituated or sensitized to test conditions over our experimental period. For example, strong habituation could have

resulted in a reduction of variance among individuals such that traits are no longer repeatable or correlated with each other. Sensitization could have resulted in additional variance within some individuals during the second assay, thus resulting in lack of repeatability between time points. Although these two factors operate in opposite directions (i.e. reducing variance or increasing variance) the end result is the same: reduced trait consistency. However, differences in consistency between personality traits in other species have also been observed, and theory suggests that differences in consistency may arise from differences in measurement techniques as well as underlying proximate mechanisms and ecological importance (Bell et al. 2009; Fratkin et al. 2013).

The strong consistency and stable structural nature of the personality trait aggression (see also Sinn et al. 2008b; While et al. 2009a, 2010; Isaksson et al. 2011; McEvoy et al. 2013), may be due to the fact that it is an aggregate measure rather than a single measure. Measurement theory suggests that aggregate measures should have greater predictive validity than singular measures, because measurement error of each single observed variable comprising an aggregate scale (random by definition) tends to be cancelled out, thus improving reliability (Epstein 1983; John and Soto 2007). In other words, exploration, activity, and boldness consistency estimates may have been higher if a reliable aggregate measure of these traits could have been captured. Alternatively, the observed differences in consistency between traits may be the result of differential selection for consistency *per se* (Dall et al. 2004; Schuett et al. 2010). Selection for consistency in personality traits might occur if there is an advantage to being predictable. For example, Schuett et al (2010) suggested that this might occur in species where mate choice has long term consequences (species that form long-term pair bonds or engage in bi-parental care, such as *Egernia*; Chapple 2003) if individuals gain benefits to choosing partners that are predictable in their behaviour or if consistency of a trait is an honest signal of quality/reproductive success (Schuett et al. 2010). The moderate consistency of exploration, activity, and boldness may indicate that flexibility (rather than consistency) has been favored in this population. Future studies will examine selection on consistency of exploration, activity, and boldness in this system; at the present time the strength of selection for consistency on these traits is unknown (see Réale et al. 2007 and reviews by Gosling and John

1999; Gosling 2001, for the ecological importance of exploration, activity, and boldness in other species).

The lack of consistency in sociability was unexpected as *Egernia whitii* are a social lizard species that live in small family groups (see While et al. 2009a, b, c). However, *Egernia* are also highly aggressive (O'Connor and Shine 2004; Langkilde et al. 2005; While et al. 2009a); males and females aggressively defend home ranges from conspecifics and tolerance of non-family conspecifics, non-pair adults and non-kin offspring, is low (While et al. 2009a, c). This high level of aggression towards non kin may affect general levels of sociability and social tolerance, perhaps resulting in the negative correlation we observed between aggression and sociability (see below). Measuring sociability in this species may therefore be inherently problematic as the default response of individuals, when confronted with conspecifics, is aggression (or outright avoidance). The exception to this is partner and offspring tolerance, perhaps if we had incorporated an individual's propensity/willingness to associate with familial individuals or neighbors, rather than unknown conspecifics, our assay might have resulted in a greater ability to identify consistency. However, it is worth noting the generalized definition that we used to define 'sociability' is "an individual's reaction to the presence or absence of conspecifics (excluding aggressive behavior)" (Réale et al. 2007). Our results illustrate the complicated and perhaps sometimes species- and context- specific nature of personality.

We observed few behavioral syndromes between any of the personality traits. Two out of 15 possible syndromes were observed: aggression and sociability were negatively correlated in females during the first assay, and activity and exploration were negatively correlated in females and males during the second. Variability in behavioral syndromes may have been related to the variability in consistency in the personality traits over time. Consistency in traits is thought to influence the strength of between-trait correlations (Stamps and Groothuis 2010). Alternatively, the general lack of syndromes observed in this *Egernia* population may have been the result of different proximate mechanisms (e.g. genetic, physiological, neuro-endocrine systems) underlying different traits rather than common proximate mechanisms which facilitate the emergence of behavioral syndromes (Sih et al. 2004a, b; Bell

2007; Sih and Bell 2008; Réale et al. 2010; Stamps and Groothuis 2010). Behavioral syndromes can form and collapse over relatively brief periods of ecological time (Bell 2005; Bell and Sih 2007; Dingemanse et al. 2007), through ontogeny (Sinn et al. 2001; Bell and Stamps 2004), or between generations (Sinn et al. 2010). Finally, Dingemanse et al. (2007) points out that behavioral syndromes should evolve in populations where natural selection favors trait co-variance. For example, both Dingemanse et al. (2007) and Bell and Sih (2007) demonstrated that behavioral syndromes varied both within- and across-populations of stickleback fish (*Gasterosteus aculeatus*), and were only present when selection pressures were high. In both cases predation pressure resulted in a behavioral correlation between boldness and aggression (Bell and Sih 2007) and aggression, activity and exploration (Dingemanse et al. 2007). Selection pressure in our studied population of *E. whittii* may not be strong enough to induce a trait co-variance.

There is often an implicit assumption that a ‘snap-shot’ is representative of longer-term patterns and that behavioral correlations present in a population are an invariant property of that population through time (Sinn et al. 2010). However, even within such a ‘snapshot’ we found variability in the structural consistency and intra-individual consistency of our personality traits, which may have resulted in variable behavioral syndromes. Whether this is due to measurement aspects of our assays (i.e., a lack of being able to aggregate observed behaviors in some assays) or is a true, inherent property of our population requires further work. Examining multiple personality traits within populations, while currently uncommon, provides exciting opportunities to expand current knowledge about the ecological and evolutionary significance of personality. Information on multiple, different personality traits in different populations or taxa is sorely needed in order for empirical verification of current theory concerning the adaptive nature of personality itself (Réale et al. 2010; Sih et al. 2012; Wolf and Weissing 2012).

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Chapter 3

Repeatable intra-individual variation in plasma testosterone concentration and its sex-specific link to aggression in a social lizard

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Chapter 4

Examining the role of testosterone in mediating short-term aggressive responses to social stimuli in a lizard.

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Chapter 5.

Maternal care in the Tasmanian echidna *Tachyglossus aculeatus* *Setosus*

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Chapter Six

The role of size and aggression in intrasexual male competition in a social lizard species, *Egernia whitii*

Abstract

Competition between males is a key component of the agonistic intrasexual interactions that influence resource acquisition, social system dynamics, and ultimately reproductive success. Sexual selection theory predicts that traits that enhance success in intrasexual competition (particularly male-male competition) should be favored. In vertebrates this often includes body size and aggression, with larger and/or more aggressive males outcompeting smaller or less aggressive conspecifics. The majority of studies consider aggression as a flexible trait which responds to local social or environmental conditions. However, aggression frequently shows considerable within individual consistency (i.e., individuals have identifiable aggressive behavioral types). Little is known about how such consistency in aggression may influence competition outcomes. We integrated a detailed field study with a laboratory experiment to examine how a male's aggressive phenotype and his size influence competitive interactions in *Egernia whitii*, a social lizard species which exhibits strong competition over resources (limited permanent shelter sites and basking sites). Individual aggression and size did not predict competition outcome in the laboratory nor did they predict home range size, overlap, or reproductive success in the field. However, winners of laboratory trial contests maintained consistent aggressive phenotypes while consistency in aggression was lost in losers. We suggest that aggression may be important in other functional contexts, such as parental care, and that alternative traits, such as fighting experience, may be important in determining competition outcome in this species.

Introduction

Competition between males over resources (including mates) is a conspicuous component of most mating systems (Andersson 1994; Shuster and Wade 2003; Jenssen et al. 2005). The outcome of this competition can have important consequences for resource acquisition, reproductive success and survival (Calsbeek and Sinervo 2002; Huyghe et al. 2005; Wong and Candolin 2005). Thus, male competition can influence the strength of both natural and sexual selection. Identifying the characteristics that influence the outcome of intrasexual male conflict is therefore central to our understanding of phenotypic evolution (Huyghe et al. 2005).

The key trait suggested to influence the outcome of agonistic interactions between males that lack weapons is body size (Maynard Smith and Parker 1971). Larger males often have an advantage over smaller males in contests (see Andersson 1994; Olsson and Shine 2000; Fairbairn et al. 2007) as size is generally correlated with strength, stamina and the ability to inflict injury (Arnott and Elwood 2009). Furthermore, large body size can be advantageous in settling contests on the basis of size asymmetries alone (Yoshino et al. 2011) reducing the need for contests to escalate into potentially costly physical encounters (Prenter et al. 2008).

Although size is considered the key trait that influences competitive ability, behavioural traits, such as aggression, can also play an important role in dictating the outcome of competitive interactions (Duckworth 2006; Fuxjager and Marler 2010; Huang et al. 2011; Kasumovic et al. 2010; Wilson et al. 2011). For example, more aggressive individuals are often better competitors for limited resources such as food, shelter and mates than less aggressive individuals (Thompson and Moore 1991; Duckworth 2006; Arnott and Elwood 2009; Herrel et al. 2009). Indeed, fighting ability is strongly influenced by an individual's innate level of aggression (e.g., Barlow et al. 1986; Thompson and Moore 1991) and aggression has been shown to influence intrasexual male contests when the difference in size between individuals is small (Arnott and Elwood 2009). In some situations, small aggressive individuals can even be dominant over larger, but less aggressive, individuals (Schulte-Hostedde and

Millar 2002; Morrel et al. 2005; Just et al. 2007). As a result, aggression has been shown to be associated with dominance and territory acquisition (Beaugrand et al. 1991; Schulte-Hostedde and Millar 2002; Young et al. 2008).

While the majority of these studies consider aggression to be a flexible trait responsive to environmental and social contexts, in many cases, aggression can be somewhat constrained within individuals (i.e. individuals have a distinctive aggressive phenotype; Sinervo et al. 2000; Gosling 2001; Sih et al. 2004a, b; Duckworth 2006; Wilson et al. 2011). Thus, individuals often show some, but limited, plasticity in their aggressive behaviour; i.e., some individuals are consistently more or less aggressive than others. This should have important implications for the role of aggression as a mediator of competitive outcomes because it limits the extent to which individuals can alter their aggressiveness within a given social context. For example, highly aggressive individuals may be constrained in their response (i.e. they potentially cannot decrease their aggression), resulting in unnecessary escalation of agonistic interactions and the risk of physical injury or even death. Additionally, if aggression is consistent, then it may act as an honest signal (Dall et al. 2005) and be an important source of information for conspecifics allowing them to adjust their own response (e.g. the role of familiarity in assessing competitors; Lopez and Martin 2001; Hyman and Hughes 2006; Price and Rodd 2006; Bierbach et al. 2011). As with body size this may be advantageous in settling contests on the basis of behavioural asymmetries, reducing the need for contests to escalate into potentially costly physical encounters.

In many species, size and aggression are linked, either positively or negatively (e.g. Sacchi et al. 2009; Fawcett and Johnstone 2010; Logue et al. 2011). For example, size and aggression can be mechanistically linked (Herrel et al. 2009). Larger body size can allow for larger muscle attachments which may, for example, enable an individual to have an increased bite force (see Herrel et al. 2009) resulting in larger individuals being more aggressive in initiating and pursuing fights as they possess the fighting ability to back up agonistic threats. Alternatively, if smaller individuals are only likely to gain resources through an attack, then this may prompt aggressive behaviour (the “Desperado effect”: Grafen 1987; Just et al. 2007 and references

therein). In these situations, size and aggression will be negatively related, with smaller individuals being more aggressive. When traits are correlated, aggression could be an important covariate of size, and vice versa, and each trait potentially mediates the influence of the other (Logue et al. 2011). In terms of phenotypic evolution, important insights into the relative importance of each trait for male success (e.g., in male-male competition over resources) can be gained from studies on species in which these traits are disentangled.

Egernia whitii is such a species. *Egernia whitii* is a medium sized viviparous lizard that lives in small family groups with adults maintaining individual home ranges which overlap to form small, stable, kin based social groups (see While et al. 2009a). There is considerable variation in the levels of social organization within populations of *Egernia* (reviewed in Chapple 2003), which has implications for male fitness. Specifically, both the sexual composition of a male's social group (monogamy vs. polygyny) and the acquisition of extra-pair paternity strongly influence variance in male reproductive success (While et al. 2011). As social organization is largely the result of competition over specific habitat characteristics, due to the necessity for substrate suitable for burrowing (Chapple 2003) and areas of high thermal quality (Langkilde et al. 2003), there should be strong selection on traits that influence a male's ability to acquire resources and subsequently social and extra-pair partners (While et al. 2011). Aggression and size are two traits that may be of particular importance in predicting male competitive success in *Egernia*. Size is often a key trait in determining the outcome of agonistic interactions in reptiles (e.g. Sacchi et al. 2009; Calsbeek and Cox 2010). *Egernia whitii*, and other *Egernia* species, exhibit sexual size dimorphism (Chapple 2003; 2005), suggesting there may be sexual selection on size in *Egernia*. Furthermore, consistent individual variation in aggression is an important predictor of social interactions in female *E. whitii*, influencing mating behaviour as well as offspring survival (Sinn et al. 2008; While et al. 2009a). Importantly, previous data suggests that size and aggression are unrelated in this species (McEvoy et al. unpublished).

To address the relative importance of size and aggression in influencing the outcome of competition, we integrated a detailed field study on the effects of male size and

aggression on home range size, overlap and male reproductive success, factors which are likely outcomes of competitive interactions in the wild, with a laboratory manipulation of resource availability (i.e. basking sites).

Methods

Study Species

White's skink (*Egernia whitii*) is a medium sized (up to 100mm snout-vent length, SVL) viviparous skink found throughout grasslands, coastal heath and forests in south-eastern Australia. We used *E. whitii* from the east coast of Tasmania, Australia (42°57' S, 147°88' E). We used a previously studied population (see While et al. 2007; Sinn et al. 2008; While et al. 2009a, b, c; While et al. 2010; 2011) for the field study and an adjacent population for the laboratory study. Individuals at both sites are found in discrete patches of open grassland in close proximity to excavated burrows or rock crevices that they use as retreat sites. *Egernia* become reproductively mature at approximately three years and have an overall lifespan of approximately ten years (Chapple 2003; While et al. 2007). *Egernia whitii* live in small family groups based on socially monogamous male/female pair bonds, with stable home ranges and approximately 25% extra pair paternity (While et al. 2009b, c).

Field Study

All field study subject lizards were part of a larger life history study that has taken place across seven subsequent reproductive seasons, 2004/05 to 2010/11 (see While et al. 2007; While et al. 2009a, b, c; While et al. 2010; 2011). All individuals in the field study population were therefore toe-clipped to allow for unique identification previous to the present study. During Sept/Oct 2007, all individuals were (re)captured via mealworm fishing and noosing. Once captured, individuals were measured for weight (± 0.1 mg) and length (snout-vent and head width and head length ± 0.5 mm using digital callipers), sex was determined via eversion of the hemipenes, and a tail tip was taken for later genetic analysis (see below). Throughout the field season (September 2007 – March 2008) detailed positional and behavioural observations of all individuals were collected using a digitized map of the study area. From this positional data, we calculated adult home ranges using a fixed-kernel analysis with a least-squares cross-validation smoothing parameter (Powell 2000) as we have in

previous work (While et al. 2009a, b, c; While et al. 2011). Specifically, we used 95 per cent isopleths to calculate total home range area and 50 per cent isopleths to calculate core home range area. An individual's 50 per cent core area is associated with permanent shelter and crevice sites from which basking, feeding and social activities are undertaken (Chapple 2003). Where home ranges did not meet 80 per cent of the asymptote, that individual's home range data was removed from further analysis (Rose 1982). Home range overlap was calculated as the number overlap of males, females and all adults for each individual's total and core kernel home range. All positional data were analysed using ANIMAL MOVEMENT (Hooge and Eichenlaub 1997).

Our methodology for identifying social pairings has been detailed elsewhere (While et al. 2009a, b, c; While et al. 2011). Briefly, social pairings were primarily determined when an adult male's core area home range overlapped any portion of a female's (or multiple females') core home range (80% of social pairs). Where no females fulfilled this criterion, a male's social grouping was assigned to the female(s) for which he had the greatest total home range overlap and there were no other males with a similar level of overlap (20% of social pairs). Males and females who did not have any other individuals overlapping their core area home range, were not observed consistently with a specific partner, or who had multiple centres of activity throughout the season were identified as floaters. These social groups were confirmed by observational data related to pair bonding collected throughout the study period (i.e. basking, mating and tolerance of offspring; see also Gardner et al. 2002; Chapple and Keogh 2006).

DNA was extracted from tail tip samples and genotyped for six microsatellite loci (EST1, EST2, EST4, EST12: Gardner et al. 1999; TruL12, TruL28: Gardner et al. 2008) using standard molecular techniques (see While et al. 2009a, b, c; While et al. 2011 for further details). Paternity was assigned using the computer program CERVUS 3.0 (Marshall et al. 1998) using the following simulation parameters: 10,000 cycles, 95% of candidate parents sampled, 90% loci typed and a genotyping error of 1% (calculated in CERVUS from our data). The one parent known option was used, with all adult males (SVL > 70mm) in the population included as possible

fathers. Paternity was assigned to the male with the highest male-female-offspring trio LOD score and the lowest number of mismatches (0 or 1) (e.g., Foerster and Kampenars 2004; Chapple and Keogh 2005). In cases where we were unable to separate two males based on the above methods (8% of cases), paternity was assigned to one of those males based on behavioural and home range observations (i.e., distance between male and female home ranges). This allowed us to exclude any males that were never seen in close proximity to the female's home range (see Foerster and Kampenars 2004; Chapple and Keogh 2005; While et al. 2011 for similar approaches). By comparing paternity data to data on a male's social pair-bond(s), we could determine whether offspring were the result of within- or extra-pair copulations.

Laboratory Competition Trials

We captured a total of 70 adult male (≥ 70 mm SVL) *E. whitii* within a one week period at the end of October/beginning of November 2008 from a population adjacent to our field study site (i.e., previously unknown individuals), and transported them back to the specifically designed terrestrial ecology facility at the University of Tasmania (see below for animal husbandry). Once in the laboratory, all individuals were weighed and measured (snout-vent length, head length and head width) and given an individual number written in non-toxic marker pen on their back for ease of identification. Lizards were given one week after the capture of the final lizard to acclimate to laboratory conditions ('acclimation week', Jones and Bell 2004; after which they were given their first aggression test (week one, see below for aggression testing protocol)). The week after this (week two), the second aggression test was conducted and the following week we commenced competition trials (week three). After the competition trial, a third aggression test was given. A minimum of five days separated each of the aggression tests and the competition trial. Order of testing for individual lizards in aggression tests, and for running paired competition trials, was random.

For the competition trial, we staged competitive encounters between two randomly paired males (N=34 trials) in a standardized competition arena with a single basking resource. Each individual was taken from their home cage and placed in one side of

the competition arena, separated from each other by partitions. The competition arena (60cm x 80cm x 40cm) was set up with a rock and basking light in the middle and two partitions separating the arena into thirds. Prior to placement in the competition arena individuals had one-hour's access to their basking light in their home cage and their temperature was taken with an infrared thermometer (Testo 805 Mini Infrared thermometer). Reptiles need to bask in order to maintain body temperatures necessary for essential metabolic processes, and access to basking sites is thus highly important. By limiting basking prior to interactions (i.e. only allowing them one hours access to home cage basking lights), and only providing a single basking site in the test, lizards should have been more likely to compete for the limited resource. Individuals were given a 10-minute acclimation period after which the partitions were removed and individuals were able to compete for access to the basking rock. Trials ran for a total of 20 minutes (excluding acclimation time) and all trials were video recorded (DSP color 1/3 inch security cameras fed to a Ganz DR16 NRT DVR recording system). We recorded time spent basking (seconds) for each individual within the trial; an individual was considered to be basking if it was on top of the basking rock directly under the light. We also observed details of physical interactions (i.e. latency to approach each other, duration of attacks). In five of 34 trials neither of the lizards basked. This was either because both lizards explored the arena but did not bask, or because the pair spent the entire 20 minutes of the trial physically fighting and neither lizard basked; these trials were excluded from further analysis. In all other trials, lizards physically fought with each other, and one lizard would access the basking rock. If one was on the basking rock and the other approached and attempted to access the rock, the two lizards would fight, and one would drive the other away and again bask on the rock. At the conclusion of 20 minutes individuals had their temperature taken a second time and were then returned to home cages. Following the conclusion of the experiment all individuals were released to their field site. We use time spent basking as our measure of competition outcome.

Conspecific Aggression Test for Field and Laboratory Tests

For lizards from the field study, we measured individual aggression twice over a four-month period, once during the mating season (September-October) and once during post-mating period (December-January). Specifically, male lizards were captured

once in Sept/Oct (N = 36) and again four months later (N=22, representing a 61% recapture rate). At both time periods, in order to minimize disruption to the population, individual males were removed from the field site for no more than 90 hours at a time. All Sept/Oct captures took place between the 20th of September and the 11th of October, but individuals were caught in ‘batches’ to minimize the time spent in the laboratory. The same procedure was employed during the Dec/Jan aggression testing, where individuals were randomly and opportunistically re-caught for a second aggression test. There was an average of 70 ± 9 days between recapture dates. Following aggression tests males were returned to their exact place of capture. For lizards used in the laboratory competition trials, we measured individual male aggression three times over a one-month period (twice prior to a competition trial, hereafter ‘aggression test one’ and ‘aggression test two’, and once after the competition trial, hereafter ‘aggression test three’).

We quantified individual aggression with a previously established conspecific aggression test (Sinn et al. 2008; While et al. 2009a; While et al. 2010; Isaksson et al. 2011). Individuals were caught in the field using a mealworm fishing technique, after which they were transported back to the specifically designed terrestrial ecology facility at the University of Tasmania. They were then housed individually in plastic terraria with opaque sides (which allowed for testing only one lizard at a time) in a room maintained at an ambient temperature of 16°C. Each terrarium was supplied with a basking light on an 8:16 hr light/dark cycle, and overhead lights on a 9:15hr light/dark cycle. Each terraria had a basking rock under the light at one end, and a shelter at the opposite end (maintained at 15 cm from the closest edge of the basking rock) with water and food (mealworms (*Tenebrio* larvae) or pureed fruit with protein powder) available *ad libitum*. Aggression tests were conducted in the afternoon between 1400 and 1700 so that lizards could obtain their preferred body temperature before trials began (Stapley 2006); all tests were conducted by either of two experimenters (randomly JM or DLS), and test order of individual lizards was randomized on each day.

Conspecific aggression tests consisted of the experimenter approaching the front of the basking container and touching the lizard with a realistic soft plasticine model of

an *E. whitii* attached to a wooden dowel. Lizards were presented with the model after a 60 second acclimation period to the presence of the observer, but only if they were found and remained on the basking rock at the start of the test. Models were then advanced to the focal lizard (snout to snout, as we have observed individuals approaching each other in the wild) and models were presented to the focal lizard until they fled to the shelter, or up to 10 times in quick succession, with the focal lizards response to the model recorded after each approach. A single trial therefore consisted of up to 10 touches within approximately three minutes (depending on focal lizards response to the model). We used an act-frequency approach to measuring behaviours in aggression tests (Martin and Bateson 1993; McEvoy et al. 2008). Four behaviours were measured: the number of touches before the lizard fled (to a maximum of 10 touches); the number of back arches (a display whereby the spine of the lizard was bent to form a concave arch); the number of times the lizard displayed with an open mouth; and the number of times the subject actively bit the model. These behaviours closely resemble those recorded in antagonistic interactions within this and other *Egernia* species (e.g. Langkilde and Shine, 2004; Langkilde et al. 2005; Langkilde and Shine, 2007) and have been observed in the wild by both JM and GW. Behaviours in tests were recorded for the entire duration of stimulus presentation with an audiocassette recorder and hand held timer. Behaviours were scored as a multiple frequency if the lizard performed that behaviour anew after each touch with the model.

As with our previous work (see Sinn et al. 2008; While et al. 2009a; While et al. 2010; Isaksson et al. 2011), the four behaviours were highly inter-correlated, loaded strongly on a single common component in Principal Components Analysis (PCA) for each aggression test and explained >58% of the variation at each time point (see Table 1). The Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy and the Bartlett's test of sphericity both indicated that all matrices were suitable for PCA (Budaev 2010). We computed aggregate unit-weighted scale scores for each individual per test, resulting in two aggression scores per individual for the field study (once in the mating season (Sept/Oct) and once post-mating (Dec/Jan)) and three aggression scores per individual for the laboratory study (twice prior to competition trial, and once after the first competition trial).

Statistical Analysis

Field Study

We first ran Pearson's correlation coefficient between male size and aggression at both time periods to examine whether size and aggression were related. We use SVL as a measure of body size in our models; SVL was also correlated to body mass and head measurements in our sample (r 's > 0.38 , p 's < 0.04). Model outcomes were consistent regardless of which measure of size was used.

We used a two-way random effects intra-class correlation coefficient (hereafter referred to as 'repeatability'; Boake 1989; McGraw and Wong 1996) to examine individual level consistency in conspecific aggression from Sept/Oct to Dec/Jan. We use the aggression score from Sept/Oct in further analysis as the time point of this measurement corresponded with the mating season when aggression is likely to exert its strongest influence on reproductive parameters.

We fitted a general linear model to examine the effect of aggression and size (SVL) and the interaction between them on male home range size. As a male's 95% isopleths of total home range size and 50% isopleths of core home range size were highly correlated ($r > 0.743$ $P < 0.0001$, $N = 28$), we chose to use only home range characteristics measured at the 95% level as this represents the total extent of males home range and all possible competitive interactions (results are qualitatively similar regardless of whether home range characteristics based on 50% or 95% isopleths are used). We fitted generalized linear models with Poisson error terms to examine the effect of aggression, size and their interaction on male and female overlap at a male's total (95%) home range and also male reproductive success (measured as total offspring) (3 separate models). For each model, total home range size, sex-specific total home range overlap, or male reproductive success was entered as the dependent variable and an individual's aggression score, size measurement, and the interaction between size and aggression were entered as predictor variables.

Table 1: Principal component loadings, including percentage of overall variation explained and Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy and the Bartlett's test of sphericity, of behaviours measured in aggression tests for field (N = 21 at Sept/Oct and N = 25 at Dec/Jan) and laboratory (N = 62) *Egernia whitii*.

	Laboratory Test One	Laboratory Test Two	Laboratory Test Three	Field Sept/Oct	Field Dec/Jan
Number of touches	0.897	0.900	0.932	0.912	0.901
Back arch	0.815	0.965	0.928	0.858	0.877
Mouth open	0.776	0.902	0.953	0.584	0.873
Bites	0.612	0.417	0.506	0.645	0.812
% variance	61	68	72	58	75
KMO	0.527	0.649	0.570	0.551	0.815
Bartlett's	$\chi^2_{(1, 6)} = 123.66,$ p = 0.0001	$\chi^2_{(1, 6)} = 167.95,$ p = 0.0001	$\chi^2_{(1, 6)} = 128.97,$ p = 0.0001	$\chi^2_{(1, 6)} = 43.34, p$ = 0.0001	$\chi^2_{(1, 6)} = 43.91,$ p = 0.0001

Laboratory Competition Trials

As with the field study, we first ran Pearson's correlation coefficient between male size and aggression for each aggression test. As above, we use SVL as our measure of body size (SVL, mass and head measurements were correlated; $r's > 0.45$, $p's < 0.001$).

For the laboratory competition trials we first examined repeatability between aggression tests one and two (prior to the first competition trial). We used the aggression scores from test two in further analyses regarding competition outcome as this test was closer to the beginning of the competition trial (results are qualitatively similar regardless of which aggression score is used). We also examined consistency in aggression between individuals based on results from the competition trial (see below), by estimating repeatability between aggression tests two and three (pre-to-post competition trial) in those individuals that basked more during the competition trial (i.e. 'winners') versus those that basked less (i.e. 'losers'). We used a repeated-measures ANOVA to test whether aggression changed depending on competition outcome (win or loss based on time spent basking). Aggression one, two and three were entered as the dependent variables with time as the within-subjects factor and win/loss as the between-subjects factor.

We used a general linear model to examine the effect of differences in size and aggression within the pairs on the competition trial outcome. As individuals within a trial were not independent of one another (2 individuals per trial), we randomly selected one individual from each trial to run the analysis, and used the difference in aggression and difference in size (between the focal individual and his competitor, i.e., each difference value can be positive or negative) to examine their relative role on influencing time spent basking ($N = 29$ after removal of trials where neither individual basked). Time spent basking was entered as the dependent variable with difference in aggression, difference in size and their interactions as predictor variables. Difference in initial body temperature was also included in the model as temperature is important to ectotherms in mediating physical ability and physiological processes, and can potentially affect competitive ability. Finally, we ran an independent samples t-test between individuals with final body temperature as

the response variable to examine whether individuals who had increased access to the basking rock as a consequence of the trial outcome achieved a higher body temperature as a result of increased access to the basking rock.

All models were run in SAS 9.1. Data were checked for violations of assumptions. Sample sizes differ slightly between tests as not all target traits could be measured for all individuals at all times. Means and standard errors are reported throughout.

Results

Field Study

Individuals from our field study were strongly consistent in their aggression scores from the Sept/Oct to Dec/Jan time periods ($\rho = 0.76$, $F_{(1,21)} = 4.18$, $p = 0.001$, $U95\%CI = 0.90$, $L95\%CI = 0.42$). However, there was no relationship between male size and aggression in the field study males (aggression during Sept/Oct to size: $r = -0.287$, $p = 0.147$, $n = 27$; aggression during Dec/Jan to size: $r = 0.208$, $p = 0.366$, $n = 21$).

A male's home range size was not influenced by his size or aggression or the interaction between them (overall GLM fit: $F_{(1,25)} = 0.12$, $p = 0.94$). Male overlap varied from 0 - 6 individuals and female overlap varied from 1 - 7 individuals; however, size, aggression and the interaction between them were not important predictors of male overlap or female overlap (Male overlap $\chi^2_{(1,3)} = 5.16$, $p = 0.16$; Female overlap $\chi^2_{(1,3)} = 3.91$, $p = 0.27$, $N = 26$ for both models). Male reproductive success in the year of this study ranged from 0 - 6 offspring sired and was not influenced by size, aggression or their interaction ($\chi^2_{(1,3)} = 1.62$, $p = 0.65$, $N = 25$).

Competition Trials

Aggression was moderately, but significantly consistent from aggression test one to two ($\rho = 0.48$, $F_{(1,61)} = 1.93$, $p = 0.005$, $U95\%CI = 0.68$, $L95\%CI = 0.14$) but not consistent between aggression test two and three ($\rho = 0.38$, $F_{(1,40)} = 1.63$, $p = 0.063$, $U95\%CI = 0.67$, $L95\%CI = -0.15$). As with the field study, there was no relationship between aggression and size (aggression test one to size: $r = -0.059$, $p = 0.640$, $n =$

65; aggression test two to size: $r = -0.229$, $p = 0.069$, $n = 64$; aggression test three to size: $r = 0.003$, $p = 0.987$, $n = 43$).

On average, there was a large difference in time spent basking between individuals within a pair, one individual was usually clearly dominant in the competition trials and as a result basked more. There was a mean basking difference of 450 seconds between those individuals that basked more (those that we termed ‘winners’ of competitive interactions) and those that basked less (those that we termed ‘losers’ of competitive interactions) (Figure 1a). This resulted in a significant difference in mean temperatures between these individuals ($t_{(56)} = 2.19$, $p = 0.03$), with a mean temperature difference of 1.2 °C between groups (Figure 1b). However, we found no effect of the difference in aggression, difference in size, difference in initial body temperature or their interactions in predicting time spent basking (overall GLM fit: $F_{(1,24)} = 1.01$, $p = 0.33$).

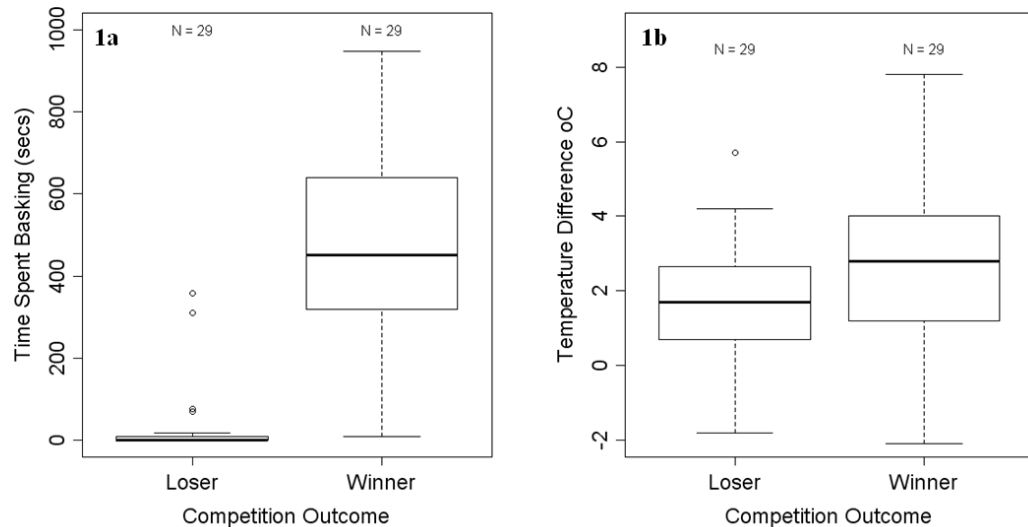


Figure 1: Difference in basking time and resultant differences in temperature between ‘winners’ and ‘losers’ in controlled laboratory competition trials with male *Egernia whiti*. Individuals who were classed as the winner in the competing pair basked for significantly more time than losing individuals with a mean basking difference between groups of 450 seconds. The mean bask time for winners was 480 seconds +/- 53.10 seconds, compared to the mean bask time for losers of 30 seconds +/- 16.63 seconds. This resulted in winners having higher body temperatures at the conclusion of the trial with the maximum winners body temperature of 26.5°C +/- 0.44 compared to 23.1°C +/- 0.23 for losers.

Closer examination of the consistency of aggression results indicated that individuals that basked more out of the pair (i.e., the ‘winners’) were highly consistent in their aggression from test two to test three (pre to post competition trials) ($\rho = 0.64$, $F_{(1,13)}=2.84$, $p = 0.03$, U95%CI = 0.88, L95%CI = -0.09). However, individuals that basked less out of the pair (i.e., the ‘losers’) were not ($\rho = 0.20$, $F_{(1,19)}=1.25$, $p = 0.31$, U95%CI = 0.69, L95%CI = -1.06; see Figure 2). Despite this, the confidence intervals associated with the repeatability estimates overlapped between winners and losers, indicating that while consistency over time was different from zero for winners, it was not statistically different to the consistency estimate for losers. There was no difference in the change in aggression over time between winners and losers ($F_{(2, 29)} = 0.80$, $p = 0.45$) indicating that competition outcome did not influence mean levels of aggression.

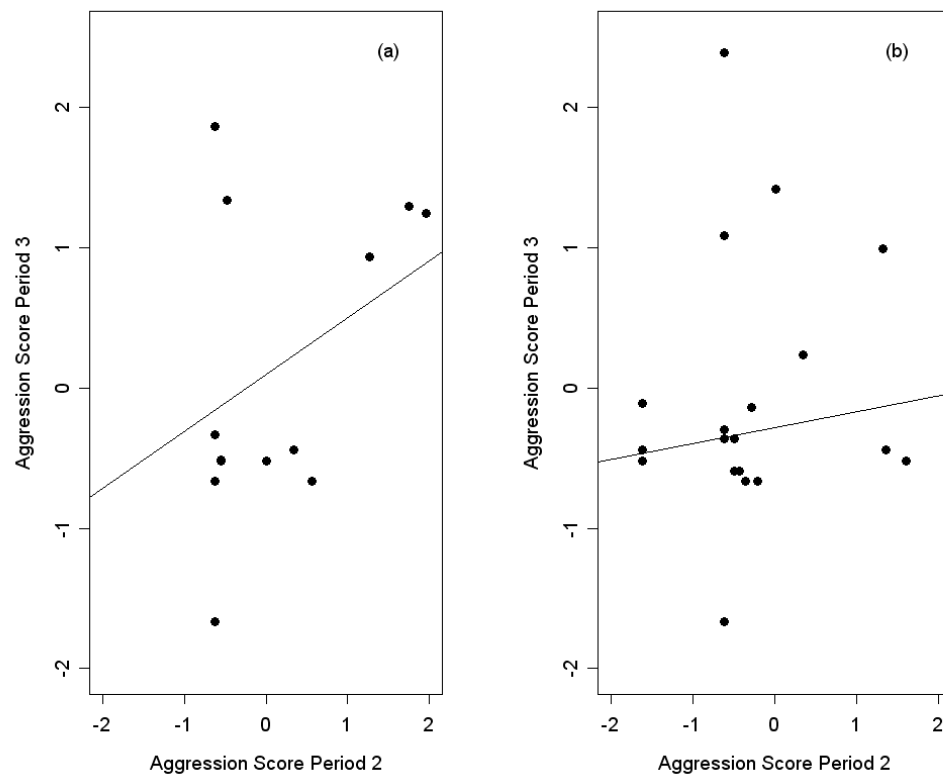


Figure 2: Scatter plot showing consistency of aggression behaviour for losers from time two to time three (Figure 2a) and winners from time two to time three (Figure 2b). Winners were consistent in their aggressive response across the time period while losers were not.

Discussion

Competition between males over resources including mates is a key component of most mating systems (Jenssen et al. 2005) and can influence both sexual and natural selection. Winners of agonistic interactions often gain primary access to resources including mating opportunities (Huyghe et al. 2005; Arnott and Elwood 2009) whereas losers often exhibit reduced performance, increased stress and reduced breeding opportunities (e.g., Langkilde et al. 2005). These outcomes of competitive interactions provide strong links between agonistic dominance and their ecological consequences (Greer 1989; Langkilde et al. 2005).

Size and aggression (often related to one another, but independent in our species) have both been suggested as being primary factors that influence the outcome of intrasexual male competition (Maynard Smith and Parker 1971; Andersson 1994; Olsson and Shine 2000; Duckworth 2006; Fairbairn et al. 2007; Fuxjager and Marler 2010; Kasumovic et al. 2010; Huang et al. 2011; Wilson et al. 2011). However, we found that in *Egernia whitii*, a social lizard species in which individuals live in saturated environments with intense competition over limited habitat resources (e.g., shelter sites (Chapple 2003) and basking sites (Langkilde and Shine 2007)), neither of these factors predicted the outcome of competitive interactions. This was true both in a large field study, where a male's aggression and size did not influence home range size, overlap or reproductive success, and in controlled laboratory trials, where size and aggression did not influence the outcome of competition over a limited resource (basking availability).

One potential explanation for this null result is that the outcomes we measured were not indicative of real competitive gains. Specifically, our field measures of habitat size may have ignored the potential important effect of habitat quality. Habitat quality is known to influence individual fitness and population dynamics across a range of species (e.g. Strong and Sherry 2000; Calsbeek and Sinervo 2002; Langkilde et al., 2007). Indeed, territory size itself, may sometimes be relatively small if habitat quality within the territory is high (Bjorneraas et al. 2012). Within the *Egernia* system, anecdotal evidence suggests that variance in habitat quality (substrate available for crevice construction) is the primary driver of variance in male

acquisition of females and thus the key resource over which individuals compete (While pers obs; see discussion in While et al. 2009b; While et al. 2011). Therefore, our focus on home range quantity as opposed to quality may have lead to erroneous conclusions regarding the role of size and aggression in predicting the outcome of competition in the field. However, despite not examining variation in habitat quality specifically, our measures of male and female overlap should still capture some component of intersexual competition in the wild. Specifically, female home range overlap represents the extent to which males can gain access to reproductive females and should largely be the result of a male's ability to acquire high quality territory (Magellan and Kaiser 2010). Conversely, male home range overlap represents the extent to which males can maintain home range exclusivity (including access to reproductive females). Both high female overlap and low male overlap should translate into increased male reproductive success and thus represent the outcome of competitive interactions, providing a thorough assessment of the competitive environment within this system. However, we found no effect of size or aggression on either of these measures or on reproductive success as measured by number of offspring sired. In the laboratory trials the winners of competitive interactions exhibited higher body temperatures at the end of the trials compared to the losers. In reptiles, the ability to maintain optimal body temperature influences a variety of fitness-related traits including immune function, metabolic rate, development rate including effects on morphology, digestive efficiency, sensory input and locomotion, foraging behaviour, sprint speed and anti-predator behaviour (Belluere et al. 1996; Angilletta et al. 2002; Herrel et al. 2007; Punzo 2007; While and Wapstra 2009; de Barros et al. 2010; Wapstra et al. 2010). Specifically, small temperature differences (e.g. 1-2°C), such as the differences observed between winners and losers in our laboratory study, should have large consequences for metabolism and behaviour (Angilletta et al. 2002; Biro et al. 2010). Given this, we therefore believe that if size or aggression were important in a competition outcome we should have detected their effects in our experiments.

The lack of an effect of size and aggression on competition outcome raises the question of what does influence male competitive ability in this species? Experience, potentially over a lifetime, may have strong effects on competitive ability (Kemp

2006; Hsu et al. 2006). *Egernia whitii* is a long-lived species which lives in saturated habitats due to specific habitat requirements, they therefore potentially engage in frequent agonistic interactions. Additionally, familiarity can play an important role in agonistic encounters. The ability to recognize individuals, and especially to recognize a rival's aggressive phenotype, may help to reduce the cost of fighting (Lopez and Martin 2001; Hyman and Hughes 2006). Gaining information about neighboring conspecifics and the likely outcome of future fights can benefit individuals by allowing them to avoid potentially costly fights, but also provide individuals with information about which neighbors pose the most serious threat (Hyman and Hughes 2006). Familiarity may play a particularly important role in a species such as *E. whitii* that maintain long-term home ranges, often with the same neighboring individuals. In both our laboratory trials (where we paired randomly chosen 'novel' individuals with one another) and in the field (where we were unable to account for previous interactions) we ignored both experience and familiarity. Accounting for the potential role of both of these components may help to further elucidate the competitive environment in this system. Additionally, as well as maintaining long term home ranges, *E. whitii* form stable, long term pair bonds with the paired male and female sharing overlapping territories. Both males and females aggressively interact with conspecifics, and both actively maintain home range boundaries. Such stable social partnerships may result in pair aggression being as, or more, important as individual aggression in maintaining home range size and overlap (as outcomes of competition). Finally, other factors, such as energetic state/reserves (see Marden and Waage 1990; Briffa and Elwood 2004; Briffa and Sneddon 2007; Reichert and Gerhardt 2011) may be more indicative of competitive success. *Egernia whitii* live in saturated habitats where interactions with conspecifics are frequent, it is possible that an individual's ability to sustain energy for multiple, frequent bouts of agonistic interaction may be more important than aggression or size *per se*.

Given the benefits to males of winning intrasexual male agonistic interactions it was somewhat surprising to find no effect of male aggression (or size) on our measures of competition. This is particularly interesting given that female aggression has several links to key social traits (e.g., promiscuity and parental care, Sinn et al. 2008; While et al. 2009a) which may have significant implications for the maintenance and

divergence of social organization via its effects on male investment in offspring (While et al. 2009b). This raises interesting questions regarding the functional significance of male aggression within this system. It is well established that aggression carries with it several significant costs related to energy expenditure and the risk of physical injury during contests (Logue et al. 2011), its links to underlying hormonal mechanisms (e.g., testosterone; Lincoln et al. 1972; Wingfield et al. 1987) as well as several physiological costs (e.g., oxidative stress; Costantini et al. 2008). All three of these costs have been linked to aggression in *Egernia whitii* (Chapple 2003; Langkilde and Shine 2004; 2007; Langkilde et al. 2005; While et al. 2010; Isaksson et al. 2011). Thus, it seems unlikely that male aggression is a selectively neutral trait within this system; this begs the question, why is there consistent variation in aggression observed in male *Egernia*? One reason may be that aggression is a carryover of female aggression. Similar arguments have been suggested to explain the presence of several sexual traits in females, including aggression (Amundsen 2000). Alternatively, male aggression may function in several additional social contexts. For example, unlike most reptile species, *Egernia* display parental care (Chapple 2003; O'Connor and Shine 2004; Sinn et al. 2008; While et al. 2009a), with offspring benefiting from delayed dispersal in terms of access to resources and potential defense against predators, including conspecifics (e.g., Bull and Baghurst 1998; O'Connor and Shine 2004; While et al. 2009a). Sinn et al (2008) showed that female *Egernia* increase aggression throughout gestation and suggest that protection of offspring from infanticide may be the key reason (see also O'Connor and Shine 2004). It is also possible that variation in aggression in males is related to variation amongst males in their ability to protect offspring. Additionally, *Egernia* generally live in saturated habitats where interactions with sympatric species are also potentially frequent. For example, Langkilde et al. (2005) showed that *Egernia saxatilis* actively exclude sympatric species such as *Eulamprus heatwolei*. Therefore, it is possible that male aggression and size is more relevant for interspecific interactions than intra-specific male competition. However, considerable additional work is required to test these alternative hypotheses related to the functional significance of male aggression within this system.

We have demonstrated consistent intra-individual variation in behaviour in our species both in this study, and in previous work (see Sinn et al. 2008; While et al. 2009a; While et al. 2010; Isaksson et al. 2011). However, in this study we also observed intra-individual behavioural plasticity which was dependent upon competitive outcome. Specifically, winners (those that spent more time basking) of competitive interactions had consistency estimates from pre – to – post competition trials that were different from losers, whereas losers had estimates that were not. While it is currently unknown how or why these differences in consistency may have occurred, inter-individual differences in intra-individual behavioural change may actually be widespread (Stamps et al. 2012). Here, the experience of the first laboratory competition trial may have influenced an individuals' subsequent aggressive expression directly through experience and increasing an individuals' information about its fighting ability (Arnott and Elwood 2009; Lehner et al. 2011) or indirectly, through altering underlying physiological and neuroendocrine mechanisms (Oyegbile and Marler 2005; Hsu and Wolf 2001; Fuxjager et al. 2010). Both direct and indirect influences of competition could affect both the level of aggression itself as well as the consistency of aggression (Dzieweczynski et al. 2012). How these effects produce differing levels of consistency for winners and losers within our system requires considerable ongoing work, however, exploring both the causes and consequences of changes in behaviour and behavioural consistency following a competitive encounter has the potential to provide an important avenue for future research.

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Ethical Standards

All research was carried out under the requirements of the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th edition, 2004 and the University of Tasmanian Animal Ethics Guidelines. All work was carried out under the University of Tasmania Animal Ethics Permit A0010061 and the Tasmanian Department of Primary Industries, Parks, Water and the Environment Permit FA 08245.

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Chapter Seven

The interplay between environment, aggression and fitness in a free-living vertebrate

Abstract

The association between phenotypic variation and environmental variation is a central theme in evolutionary biology as it reflects the way in which organisms adapt to their surrounding environment. Behaviour is a key factor mediating an individual's interaction with its environment. Therefore, how individuals behaviourally respond to their environment potentially has important consequences for individual fitness and population dynamics. Aggression in particular is both influenced by, and influences, an individual's physical environment and individual differences in aggression have strong and persistent effects on fitness-related traits. We examined the links between environment, individual behaviour, and fitness in a social lizard species *Egernia whitii*. We found that there was an association between aggression and temperature, with more aggressive individuals occurring in warmer habitats. We suggest that this is a result of more aggressive individuals being better competitors for these high quality areas. In terms of reproductive output, the importance of male aggression in this system appears to be context-dependent: in resource limited areas (in terms of percentage of rock cover), more aggressive males had a higher reproductive output than less aggressive males. Male reproductive output in high resource areas (high percentage of rock cover) did not appear to be aggression dependent. Female reproductive effort was determined by the amount of rock cover in her territory and her aggression. This study represents a first step in disentangling the complex relationships between environmental variation and individual behavioural variation in determining fitness and population dynamics.

Introduction

The association between phenotypic variation and the environment is a central theme in evolutionary biology. It reflects the way in which organisms respond to their surrounding environment and the consequence thereof for micro-evolutionary mechanisms that lead to phenotypic diversification (Rieseberg et al. 2002; Kingsolver and Pfennig 2007). However, our understanding of such feedbacks is poor because few studies have quantified the effects of environmentally induced changes in phenotypic trait distributions on population processes (e.g., reproductive output, survival) and their consequences for evolutionary response (Fussmann et al. 2007; Kokko and Lopez-Sepulcre 2007; Pelletier et al. 2009).

Behaviour is a key factor within this framework because it is the first aspect of an organism's reaction to the environment and thus, can play a more active role in its response (Duckworth 2009). Even when levels of behavioural expression are relatively inflexible or consistent within individuals – a common observation in vertebrates (Sih et al. 2004) – the reactivity of behaviour provides an important mediator between environmental variation, population growth, and ultimately evolutionary change (Duckworth 2009). For example, Duckworth (2006) showed that in the Western Bluebird (*Sialia mexicana*) competition over limited tree cavities resulted in the sorting of aggressive and non-aggressive males into different habitats. The result of which was differential selection on morphological traits demonstrating that behaviour can affect evolutionary diversification via its interaction with local ecological conditions (Duckworth 2009). Studies such as these are rare and thus, the role of behaviour in linking ecological and evolutionary dynamics has rarely been put under empirical scrutiny. To address this we need studies where we can both identify the factors that influence behaviour at the level of the individual and link these with population level processes that could ultimately lead to evolutionary diversification (Plotkin 1988; Huey et al. 2003; West-Eberhard 2003; Losos et al. 2004; Sol et al. 2005).

Aggression is a particularly important behavioural trait which is likely to influence eco-evolutionary dynamics. Aggression influences a variety of socially important traits including territory acquisition and defense (e.g. Schulte-Hostedde and Millar

2002; Duckworth 2006), intra-sexual competition (e.g. Huang et al. 2011; Wilson et al. 2011), mate acquisition (e.g. Duckworth 2006; Schuett et al. 2011), parental care (e.g. O'Connor and Shine 2004; Sinn et al. 2008), promiscuity (e.g. While et al. 2009a), foraging ecology (e.g. Pruitt and Ferrari 2011) and anti-predation behaviour (e.g. Kazama and Watanuki 2010). The distribution of individuals with varying aggressive phenotypes is also likely to vary spatially and temporally either as a result of direct (plastic) responses to environmental/social conditions and/or as a result of response to selection (Sih et al. 2012; Wolf and Weissing 2012). Therefore, changes in both the distribution and the frequency of aggressive phenotypes over time or space will produce a dynamic environment in which the relationship between the environment, aggression, and selection are ever changing (Chesson and Rosenzweig 1991; Mougeot et al. 2003; Duckworth 2006). An individual's aggression phenotype is thus an obvious candidate to play a key role in mediating the consequences of environmental variation for the ecological and evolutionary trajectory of populations (Mougeot et al. 2003; 2005; Le Galliard et al. 2005).

In this study, we aimed to take the first steps in elucidating the relationships between aggression, environmental variation (both biotic and abiotic), and fitness (reproductive output) within a wild vertebrate population. To do this we used a lizard species, *Egernia whitii*. *Egernia* are typically found in highly saturated environments, characterized by intense competition over a limited number of permanent shelter sites and high levels of conspecific aggression (Chapple 2003; Langkilde et al. 2003; While et al. 2009b, c). The ability of individuals to acquire high quality habitat that allows access to these permanent shelter sites will therefore be paramount to an individual's fitness. However, the consequences of habitat quality on an individual's fitness will depend on behavioural responses, and in particular male and female aggression levels. Indeed, aggression is an ecologically important behavioural trait that will largely dictate the outcome of competitive interactions both between and within the sexes. *Egernia* exhibit strong intra-individual consistency in aggression (Sinn et al. 2008; While et al. 2009a; McEvoy et al. 2013). The consistent variation in behavioural phenotypes within the *Egernia* system may both be a cause and consequence of eco-evolutionary feedback loops between environmental variation, reproductive success, and selection. To test this we i) examined the potential

environmental factors that influence aggression in this system, and then ii) considered how aggression, in conjunction with key environmental characteristics, influence male and female reproductive success.

Methods

Study Species

We used a previously studied population of *E. whitti* (see While et al. 2007, While et al. 2009a; McEvoy et al. 2013) from the east coast of Tasmania, Australia (42°57' S, 147°88' E) for this study. Individuals are found in discrete patches of open grassland in close proximity to excavated burrows or rock crevices that they use as retreat sites. *Egernia whitti* populations are fairly saturated due to strict habitat requirements of appropriate burrow sites and basking retreats. Individuals live in small family groups based on socially monogamous male/female pair bonds, with stable home ranges and approximately 25% extra pair paternity (While et al. 2009b, c). They become reproductively mature at approximately three years and have an overall lifespan of approximately ten years (Chapple 2003; While et al. 2007).

Field Study

All subject lizards were part of a larger life history study (see above) and all individuals were therefore toe-clipped to allow for unique identification. During Sept/Oct 2010 all individuals were (re)captured and measured for weight (± 0.1 mg) and length (snout-vent and head width and head length ± 0.5 mm using digital callipers), sex was determined via eversion of the hemipenes, and a tail tip was taken for later genetic analysis (see below). Throughout the field season (September 2010 – March 2011) detailed positional and behavioural observations of all individuals were collected using a digitized map of the study area. From this positional data, we calculated adult home ranges using a fixed-kernel analysis with a least-squares cross-validation smoothing parameter (Powell 2000). Specifically, we used 95 per cent isopleths to calculate total home range area and 50 per cent isopleths to calculate core home range area. An individual's 50 per cent core area is associated with permanent shelter and crevice sites from which basking, feeding and social activities are undertaken (Chapple 2003). Where home ranges did not meet 80 per cent of the asymptote, that individual's home range data was removed from further analysis

(Rose 1982). All positional data were analysed using ANIMAL MOVEMENT (Hooge and Eichenlaub 1997).

At the end of gestation, all pregnant females in the population (N = 26) were captured, measured for length ($\pm 1\text{mm}$) and weight ($\pm 0.1\text{mg}$) and returned to the specifically designed terrestrial ecology facility at the University of Tasmania to give birth. Females were housed individually in plastic terrarium in a room maintained at an ambient temperature of 16 °C. Each terrarium was supplied with a basking light on at 9:15hr light/dark cycle and overhead lights on a 8:16hr light/dark cycle. Each terraria had a basking rock under the light at one end and a shelter at the opposite end (maintained at 15 cm from the closest edge of the basking rock) with water and food (*Tenebrio* larvae or pureed fruit with protein powder) available ad libitum. At birth, offspring were temporarily removed from their mother to be marked, have their weight ($\pm 0.1\text{mg}$), SVL and total length ($\pm 1\text{mm}$) recorded, and a portion of their tail tip taken for genetic analysis. We were unable to identify offspring sex as juvenile female *Egernia* retain their hemipenes until well after birth (Chapple 2003). Within 3 days of birth, offspring were released with their mother at their mother's site of capture.

To collect data on male reproductive success we collected tail tip samples from all individuals (including offspring born in the laboratory), extracted DNA and genotyped all samples for six microsatellite loci (EST1, EST2, EST4, EST12: Gardner et al. 1999; TruL12, TruL28: Gardner et al. 2008) using standard molecular techniques (see While et al. 2009a; b; c; While et al. 2011 for further details). Paternity was assigned using the computer program CERVUS 3.0 (Marshall et al. 1998) using the following simulation parameters: 10,000 cycles, 95% of candidate parents sampled, 90% loci typed and a genotyping error of 1% (calculated in CERVUS from our data). The one parent known option was used, with all adult males (SVL > 70mm) in the population included as possible fathers. Paternity was assigned to the male with the highest male-female-offspring trio LOD score and the lowest number of mismatches (0 or 1) (e.g., Foerster and Kampenars 2004; Chapple and Keogh 2005). In cases where we were unable to separate two males based on the above methods (8% of cases), paternity was assigned to one of those males based on

behavioural and home range observations (i.e., distance between male and female home ranges). This allowed us to exclude any males that were never seen in close proximity to the female's home range (see Foerster and Kempeneers 2004; Chapple and Keogh 2005; While et al. 2011 for similar approaches).

Habitat Characteristics

During October 2010 we superimposed a grid system of 5m x 5m grids over the field site of our natural population. Within each 5m x 5m grid, we recorded a number of habitat characteristics in three randomly placed 1m x 1m grids. For each 1m x 1m grid we recorded percentage of rock cover; percentage of ground vegetation cover (in the form of grass tussocks, *Gahnia grandis*, *Lepidosperma* sp) and heterogeneity of the grid square (from 1 to 5, with 1 representing a homogeneous grid and 5 representing highly heterogeneous grid). Using a hand-held spherical densitometer (Lemmon 1956), we also estimated canopy cover and canopy cover from a lizard perspective (60 cm above the ground, taking into account low-growing shrubs and bushes that will shade aspects of lizard's home range and that standard canopy cover measurements will not incorporate) and recorded presence/absence of fallen logs and branches and percentage of low-growing shrubs and bushes (common teatree: *Leptospermum scoparium scoparium*; spreading pinkberry: *Laptocophylla divaricata*; erect guineaflower: *Hibbertia riparia*; prickly box: *Bursaria spinosa*). We then averaged these three random grid squares to obtain an overall measure of the habitat characteristics in each 5m x 5m grid square.

We used Principal Components Analysis (PCA) to determine associations between the physical habitat variables (Tabachnick and Fidell 1996). Habitat variables were standardized in order to avoid spurious relationships arising from variables measured on different scales (Field 2009). The number of principal components retained was based on eigenvalues > 1, a scree plot, and interpretability (Cattell 1966; Zwick and Velicer 1986; Budaev 2010). The extracted Principal Components were then used as independent variables in subsequent analysis involving habitat variables. The first Principal Component, hereafter referred to as Habitat Component One and comprising mainly vegetation variables, explained 41% of the variation in the data and was comprised of positive values of the variables 'structural complexity',

‘percentage of total vegetation cover (grass tussocks)’, ‘canopy cover’, ‘lizard canopy cover’, ‘fallen logs’, and the specific plant species ‘erect guineaflower’, and ‘spreading pinkberry’. The second Principal Component, hereafter referred to as Habitat Component Two and comprising primarily the variable percentage of rocks, explained a further 15% of the variation in the data and was comprised of positive values of the variables ‘rocks’, ‘spreading pinkberry’ and ‘fallen logs’ (see Table 1). The Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy and the Bartlett’s test of sphericity indicated that all matrices were suitable for PCA (KMO = 0.804; Bartlett’s $\chi^2_{(1, 45)} = 1215.00$, $p = 0.0001$; Budaev 2010). We created aggregated unit-weighted scores based on these two habitat components for each grid square within the site.

Table 1: Principal component loadings, including percentage of variation explained, of the measured habitat variables.

	Component One	Component Two
%Rocks	-0.039	0.775
Structural complexity	0.852	-0.052
%Vegetation cover	0.897	-0.134
Canopy cover	0.677	-0.156
Lizard canopy cover	0.891	-0.219
Spreading pinkberry	0.395	0.468
Fallen logs	0.398	0.443
Erect guineaflower	0.450	0.299
<i>% variation explained</i>	41.3	15

Across our field site, in approximately every second 5m x 5m grid square, we placed a temperature recording Ibuttons™. Ibuttons™ were placed in the field during mating (beginning October) and left until the end of female gestation (mid-January) and were programmed to record the temperature every hour. For grid squares that did not have Ibuttons™ recording temperature, we took an average of the surrounding four grid squares to provide temperature information for the missing square. To represent the thermal quality of the site we calculated daily (9am-6pm) average temperature from the hourly data and then calculated the monthly daytime average temperature (for

October, November, December and January). All of the monthly daytime average temperatures were highly inter-correlated (Pearson's correlation coefficient all r 's > 0.45 , all p 's < 0.001). We therefore use October average daily temperature, hereafter referred to simply as temperature, in further analysis, because this measure was taken in the mating season, during which the acquisition of copulations is undertaken.

To determine habitat and temperature information for each individual lizard we determined which and how many grid squares an individual lizard's total home range (95% isopleths) covered. We then averaged habitat and temperature information across the grid squares in each lizard's home range to create three environmental scores for each lizard; habitat component one, habitat component two and temperature (October daily average).

Conspecific Aggression Assay

Conspecific aggression testing followed the procedures outlined in Sinn et al. (2008), While et al. (2009a; 2010), Isaksson et al. (2011) and McEvoy et al. (2013) for the same species. Male and female adult lizards (33 males and 22 females) were caught in the field in March 2011 and transported back to the specifically designed Terrestrial Ecology facilities at the University of Tasmania. They were then housed individually in plastic terraria with opaque sides (which allowed for testing only one lizard at a time). Aggression assays were run in the afternoon between 1400 and 1700 so that lizards could obtain their preferred body temperature (Stapley 2006).

Conspecific aggression assays consisted of the experimenter approaching the front of the home terraria and touching the lizard with a realistic soft plasticine model of an *E. whitii* attached at the end of a fishing rod. Lizards were presented with the model after a 60 second acclimation period to the presence of the observer, but only if they were found and remained on the basking rock during the acclimation period. Subjects were touched up to 10 times on the snout by the model or until they fled into or on top of the shelter. We used an act-frequency approach to measuring behaviours in aggression assays (Martin and Bateson 1993). Four behavioural variables were measured: number of touches before the lizard fled (to a maximum of 10 touches); number of back arches (a display whereby the spine of the lizard was bent to form a

concave arch); the number of times the lizard displayed with an open mouth; and the number of times the subject actively bit the model. These behavioural variables closely resemble those recorded in antagonistic interactions within this and other *Egernia* species (e.g. Langkilde and Shine 2004; O'Connor and Shine 2004; Langkilde and Shine 2005; Langkilde et al. 2005; Langkilde and Shine 2007; McEvoy et al. 2013) and have been observed in the wild by both GW and JM. Behavioural variables in assays were recorded for the entire duration of stimulus presentation with an audiocassette recorder. Variables were scored as a multiple frequency only if the lizard performed that behaviour anew after each touch with the model.

As with our previous work (see above) the four behaviours were highly inter-correlated, loaded strongly on a single common component in Principal Components Analysis (PCA) and explained > 70% of the variation. The Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy and the Bartlett's test of sphericity both indicated that all matrices were suitable for PCA (KMO = 0.600; Bartlett's $\chi^2_{(1, 6)} = 166.55$, $p = 0.0001$; Budaev 2010). We computed aggregate unit-weighted scale scores for each individual. Each individual was released at point of capture at the conclusion of aggression assays.

Statistical Analysis

All data was assessed for normality and no transformations were deemed necessary. All data was analyzed in SAS version 9.2 for Windows.

We first checked for relationships between our habitat variables by running Pearson's correlation coefficients. The only variables that were related to each other were Habitat component one (vegetation) and temperature ($r = -0.410$, $p = 0.002$, $n = 57$). However, this correlation was below 0.7 and we thus include both variables in the models below (Tabachnick and Fidell 1996).

We then examined whether there was a relationship between key habitat characteristics (habitat component one, habitat component two and temperature) and an individual's aggression phenotype or their size (SVL). We ran two general linear

models with aggression or size as the dependent variables and sex, habitat component one, habitat component two and temperature as our independent variables. Due to sample size limitations, we include only two-way interaction terms including sex. We assessed the model, removed non-significant terms and re-ran the model.

We were then interested in whether individual aggression, size, or any of our three habitat variables predicted an individuals' reproductive output. Size is often thought to be a predictor of the outcomes of competition and can be influential in enabling individuals to secure better quality habitat and access to resources, thus potentially improving reproductive success (Maynard Smith and Parker 1971; Andersson 1994; Olsson and Shine 2000). We therefore include size (SVL) as a variable in our analysis. For males, we ran two generalized linear models with Poisson distributions and total offspring number as the dependent variable. In our first model, habitat component one, habitat component two, temperature and aggression were entered as our independent variables. For the second model, we re-ran the same model but replaced aggression with size. In both models, we included all two way interactions that include either aggression or size.

There is little variance in reproductive output (clutch size) in female *E. whitii* (individuals are constrained to having between 1 – 4 offspring, Chapple 2003 and in our population the majority have 2 or 3 offspring). For females we therefore used relative clutch mass as a measure of reproductive effort. Relative clutch mass is calculated by taking an individual females total clutch mass and dividing this by her post-birth mass (Shine 1980). As female size is a known predictor of reproductive effort, with larger females having larger clutch masses (Vitt and Congdon 1978; Shine 1980; Shine 1992), relative clutch mass is a measure of the effort a female puts into reproduction independent of her size. We ran two models (with size and aggression run separately) with relative clutch mass as our dependent variable, and our four traits of interest (aggression/size, habitat component one and two, and temperature) as our independent variables. As above, due to limited sample size we include interaction terms with aggression/size only.

Results

We found a positive relationship between an individuals' aggression and the average temperature of their home range ($F_{(4,45)} = 8.60$, $p < 0.01$; Figure 1). This pattern was consistent across both sexes. Neither habitat component one (vegetation) nor habitat component two (percentage of rocks) was related to aggression (all p 's > 0.30). Size (SVL) was not related to any of our habitat variables (all p 's > 0.08).

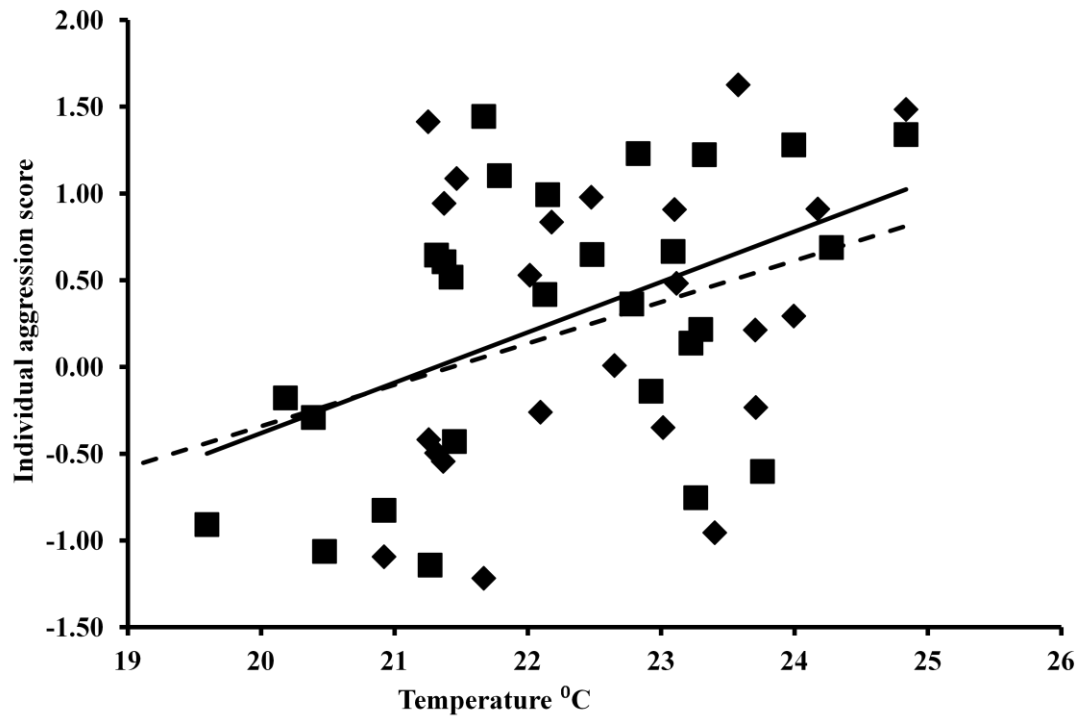


Figure 1: The relationship between temperature and individual aggression in male and female *Egernia whitii*. Females are presented in diamonds with a regression line, and males are presented in squares with a solid regression line.

Reproductive output in males was predicted by an interaction between aggression and habitat component two (rocks) ($\chi^2_{(1, 21)} = 10.54$, $p < 0.01$). Specifically, for males in areas with a low percentage of rocks, higher levels of aggression were positively related to reproductive output (Figure 2). In contrast, for males in areas with a high percentage of rocks, aggression had no effect on reproductive output (Figure 2). To examine this more closely, we re-coded the continuous variable rocks into a dichotomous variable. Habitat component two (rocks) ranged from -0.77 to 1.40, individuals with a score of equal to or lower than 0.32 on this variable were therefore classed as being in a low-rock environment, and individuals with a score of equal to

or above 0.42 were classed as living in a high-rock environment. We then ran a further two generalized linear models with Poisson distribution terms and looked at whether individual aggression was important in predicting total reproductive output for those individuals found in either high rock or low rock environments. As was suggested from our visualization of the first model, we found that for those individuals holding territories in low rock areas, there was a trend for aggression to be important in predicting reproductive output (although this failed to reach statistical significance; $\chi^2_{(1)} = 3.44$, $p = 0.06$). In contrast, aggression did not influence reproductive output in those individuals that held territories with a high rock percentage ($\chi^2_{(1)} = 1.12$, $p = 0.31$). For the model with size, none of our variables were important in determining male reproductive output (all p 's > 0.06).

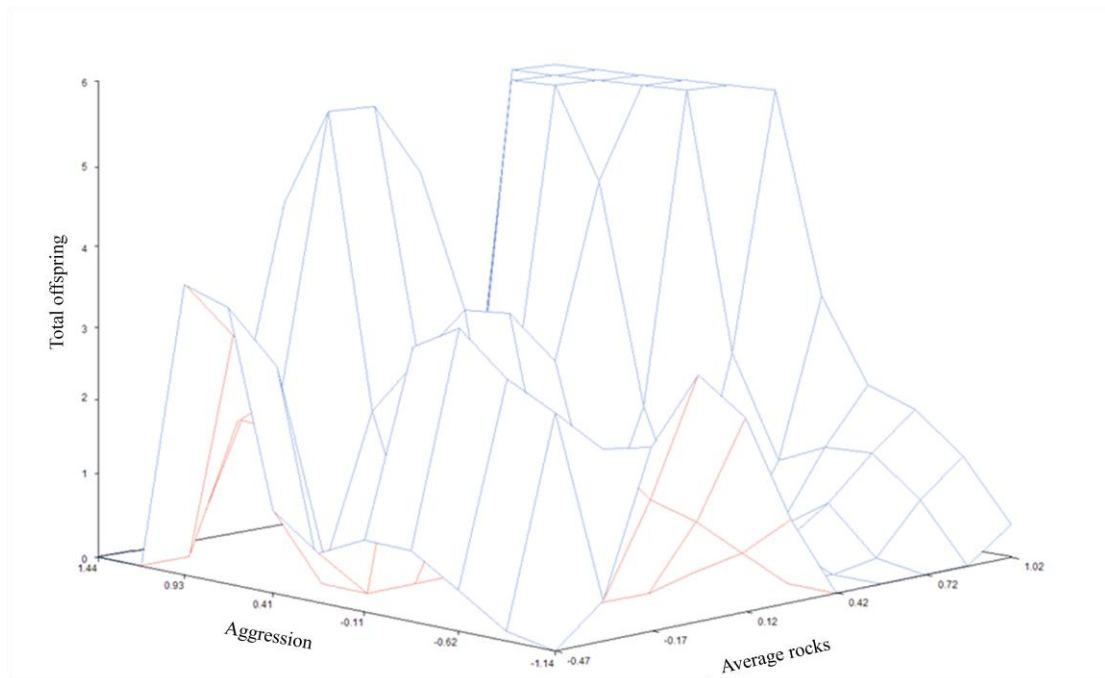


Figure 2: Spline plot of the interaction between individual male aggression and the average percentage of rocks in an individual male's territory in predicting male reproductive output.

In females, the percentage of rocks in a female's territory and her aggression influenced relative clutch mass (rocks: $F_{(4,15)} = 5.18$, $p = 0.03$, Figure 3a; aggression: $F_{(4,15)} = 6.17$, $p = 0.02$, Figure 3b). None of the other variables influenced relative clutch mass.

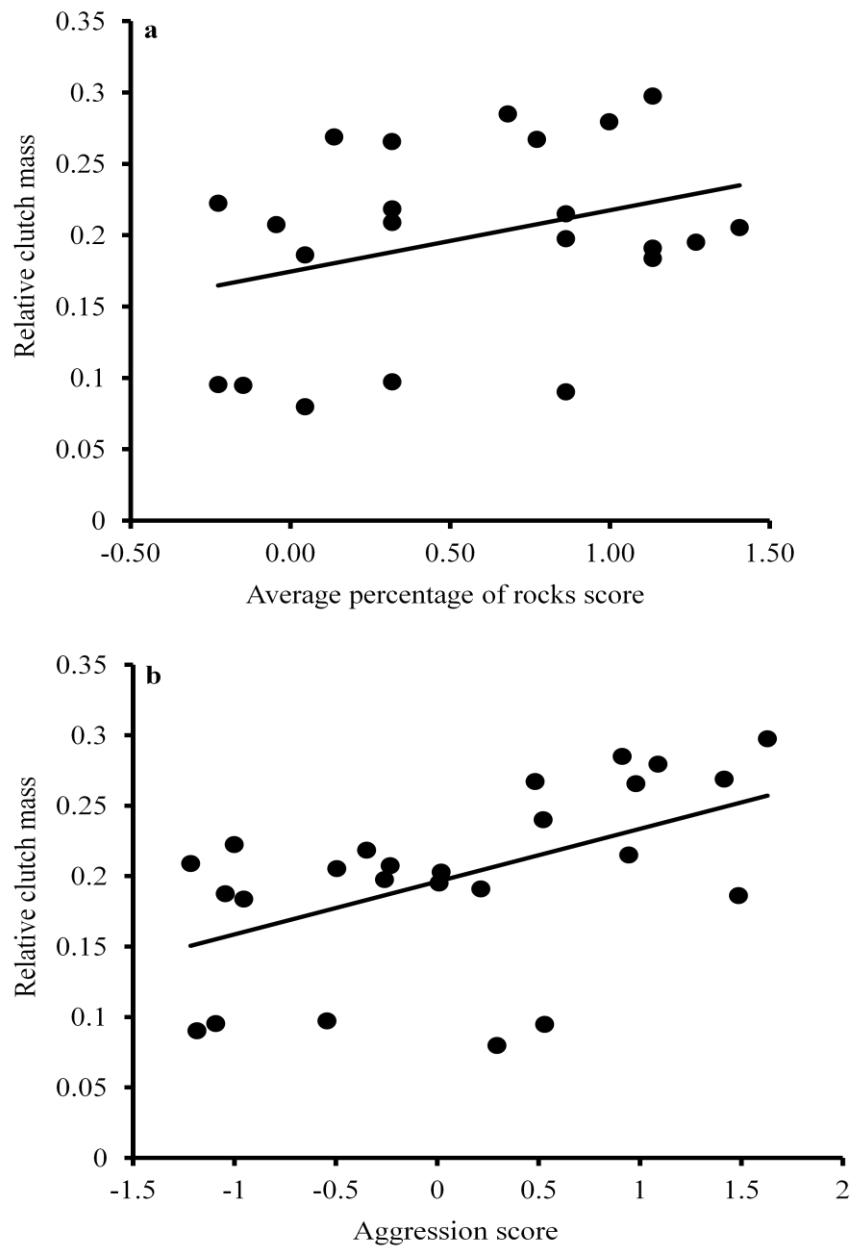


Figure 3: The relationship between relative clutch mass and (a) the average percentage of rocks in a female's territory and (b) her individual aggression score in *Egernia whitii*.

Discussion

The links between environment and behaviour and fitness are complex. Behaviour provides a mechanism through which individuals react to their environment, and both behaviour and the environment influence population dynamics and growth, leading to evolutionary change (Duckworth 2009). Understanding these links is therefore crucial for our understanding of evolutionary processes. This study represents a first step in examining these links within a free-living vertebrate. We examined the role of environmental variation in determining individual phenotypic differences (in the form of aggression and size) and how these phenotypic differences, coupled with environmental variation, influenced individual fitness. We found that aggression in both sexes was positively related to temperature. We also found that male reproductive output is predicted by the interaction between his aggressive phenotype and the percentage of rocks across his home range. Female reproductive effort is determined by both the average number of rocks in her territory and her aggressive phenotype. We discuss these results below in the context of *Egernia* life history and population dynamics.

There was an association between an individual's aggression and the thermal quality of their habitat, with areas of high thermal quality (warmer areas) containing individual's that were, on average, more aggressive. Although our analysis did not allow us to disentangle cause and effect in this relationship, we suggest two possible pathways via which this relationship may occur. Environmental effects, such as temperature, experienced during ontogeny can shape the development of behavioural traits and influence individual behavioural phenotypes as an adult (Stamps and Groothuis 2010a; b). Therefore, variation in the thermal quality of habitats within the site might be a cause of individual aggression as a result of developmental plasticity. However, as *E. whitii* disperse as sub-adults and establish adult territories in areas separate from their natal range (GMW pers obs), the temperatures they experience as adults are unlikely to be closely correlated with those they experience as juveniles. Alternatively, the relationship between aggression and temperature may be due to competition for access to the high quality habitat. Temperature influences a variety of fitness-related traits in reptiles (e.g. Belliure et al. 1996; Angilletta et al. 2002; Wapstra et al. 2010), thus, areas of high thermal quality will be an important resource

(Langkilde et al. 2003; Stapley 2006). This is particularly true for females, as temperature can have important implications for offspring phenotype and fitness (e.g., birthdates, increased mass at birth, faster growth rates, and increased locomotor performance; Wapstra 2000; Shine and Olsson 2003; Itonaga et al. 2012). Therefore, individuals may be competing for access to high quality (thermal) resources and it is more aggressive individuals that are more successful in obtaining these areas and consequently experience higher daily average temperatures. Our previous work suggested that aggression is unimportant for intra-sexual competition over territory size in this species (McEvoy et al. 2013). These results suggest that it may be territory quality, rather than size, that individuals are competing over (see also Strong and Sherry 2000; Calsbeek and Sinervo 2002; Langkilde et al. 2007; Bjørneraas et al. 2012).

These results suggest that there may be a sorting of individuals into different habitat types based on their aggressive phenotypes. More aggressive individuals appear to live in warmer areas with lower vegetation cover (based on the correlation between temperature and habitat component one). In contrast, less aggressive individuals settle in cooler areas with higher vegetation cover. Selection regimes induced by environmental pressures, even those at the micro-habitat level, can influence phenotypic evolution (e.g. Losos 1990; Beuttell and Losos 1999; Duckworth 2009). In reptiles, micro-habitat differences, including temperature, influence various aspects of individual phenotypes such as morphology (limb length, head size), metabolic rate and behaviour, including anti-predator response and foraging mode (e.g. Belliure et al. 1996; Clark et al. 2006; Cooper and Wilson 2007; Lailvaux 2007; Goodman et al. 2008; Kaliontzopoulou et al. 2010). While further research is needed to elucidate these patterns in *E. whitii* (we only looked at the relationship between environmental variables and total size, i.e. snout-vent length), this result does suggest that the interaction of behaviour and the environment may influence selection regimes experienced by individuals in a non-random manner with important consequences for ongoing phenotypic evolution in this species.

We found that a male's reproductive output is determined by the interaction between his aggression and the average percentage of rock cover across his territory. An

important resource for *Egernia* is crevice availability. In fact, this is thought to be the key driver of variance in male acquisition of females and thus reproductive success (see discussion in While et al. 2009b; While et al. 2011). Our estimate of percentage of rock cover is a crude measure of crevice availability as individuals often utilize crevice spaces between and under rocks as burrow and retreat sites (Chapple 2003; Langkilde et al. 2003; Langkilde and Shine 2004; Croak et al. 2008). These same attributes may make areas of high rock percentage attractive to females. In areas of low rock cover, our data suggests that males' with a higher aggressive phenotype compared to conspecifics have a higher reproductive output.

Aggression influences a number of outcomes associated with male reproductive success, including territory defense, resource acquisition and access to females (Marler and Moore 1988; Schulte-Hostedde and Millar 2002; Duckworth 2006; Schuett et al. 2011). In areas with a lower percentage of rocks, the ability to attract and defend mates may become more important than when rock cover is more plentiful (i.e. context-dependence of aggression; see also Johnson and Sih 2005, Bell 2007, Geange and Stier 2010). It may be that more aggressive individuals do better in this more competitive environment. In comparison to those individuals in areas of high rock cover, high levels of aggression may hold less importance. A higher percentage of rocks and associated rock crevices results in a greater diversity of resources and refuges, and decreases the importance of aggression required to secure access to these resources (Barley and Coleman 2010, Geange and Stier 2010). Barley and Coleman (2010) found that in convict cichlids (*Archocentrus nigrofasciatus*), individuals in low-structure habitats spent more time involved in aggressive behaviours (chasing and duration of chase) as well as displayed more aggressive behaviours (number of chases and bites). This impacts the amount of time and energy individuals have available for other demands, such as reproduction. In order to determine how aggression functions to increase reproductive output under varying environmental conditions, ideally we need manipulative experiments altering both environmental levels and aggressive phenotypes.

We found that female reproductive effort was dependent on both the average percentage of rocks in a females' territory and individual female aggression. Both

individuals in areas with a higher average percentage of rocks and more aggressive individuals had a higher reproductive effort. The importance of rocks to females is likely to be similar to that of males: a higher percentage of rocks and associated rock crevices results in a greater diversity of resources and refuges, representing better quality habitat. Similar studies in a number of other reptile species have shown that female reproductive effort can have strong links to the availability of resources. This could be via both direct and indirect means. First, a direct influence of rock cover on female reproductive effort could be a consequence of those areas having a greater density (or quality) of food items available and thereby influencing nutrition intake prior to and during gestation. Alternatively, as *Egernia* employ a range of foraging tactics including ambush predation (Hickman 1960; Duffield and Bull 1998; Arena and Wooller 2003; Clemann et al. 2004; Pavey et al. 2010), areas of high rock percentage with a greater variety of refuge sites provide females with more opportunities to catch insects, thereby increasing nutritional intake prior to and throughout gestation. Nutrition intake prior to and during gestation is known to influence a variety of offspring characteristics (Massot and Clobert 1995; Warner et al 2007; Bonnet et al. 1998; Cadby et al. 2011; Bleu et al. 2012; Itonaga et al. 2012) and measuring food availability, in particular insect availability, is therefore an important variable that should be considered in future studies. Second, areas of high rock percentage could indirectly influence female reproductive effort, if females facultatively alter their reproductive effort in response to habitat quality (e.g., females may adjust reproductive effort and/or outcomes of effort such as offspring size to conditions or resource availability; Wapstra and O'Reilly 2001; Olsson and Shine 2002; Marshall and Uller 2007; Cadby et al. 2011). As *E. whitii* maintain long-term home ranges (i.e. over multiple years) (While et al. 2009b, c; 2011), females may be able to accurately assess the level of resources available and thus facultatively adjust their input to match these conditions. Although teasing apart these mechanisms will be difficult, they both suggest a positive effect of habitat quality on female reproductive effort, as is shown here.

Female aggression was also found to influence female reproductive effort independently of habitat quality. This may occur if aggression is important in enabling individuals to compete for the above-mentioned resources (Woodley and

Moore 1999). Alternatively, aggression could be integrated with a number of physiological mechanisms including metabolism, the endocrine system or immune responses, all of which influence life-history traits (i.e. pace-of-life syndrome: Biro and Stamps 2008; Réale et al. 2010; Careau and Garland 2012). This can result in aggression influencing female reproductive effort through its relationship with metabolic rate. An individual's metabolic rate will dictate the amount of energy that they can invest in reproduction (as opposed to other activities) as well as influence survival which can affect decision-making (in terms of current vs. future reproductive effort) (Réale et al. 2010). The role of aggression in influencing reproduction may also be related to density as selection on aggressiveness can be density dependent (Mougeot et al. 2003; 2005; Barley and Coleman 2010). The inter-relationships between aggression, density and other phenotypic characteristics influence life-history strategies, thus illustrating how the ecological context affects the relationship between behaviour and fitness (Réale et al. 2010; Careau and Garland 2012). Careau and Garland (2012) have advocated that studies in reptiles, and squamates in particular, will be highly promising for understanding the links between personality, energetics and performance (including fitness) due to the established knowledge base of how selection acts on individual performance and life history traits (including at the micro-habitat level). Further research considering these inter-relationships will be important for understanding the role that female aggression plays in mediating reproductive effort.

Disentangling the complex and dynamic links between behaviour and the environment in influencing reproductive success is important to our understanding of population and eco-evolutionary dynamics. Even a single population of a single species occupies a diverse natural environment with fine scale environmental variation (Wilson 1998). This environmental variation is likely to influence a variety of individual level characteristics which will affect population dynamics via spacing of differing phenotypes, dispersal, resource acquisition, conspecific interactions and fitness. In this study we have demonstrated that aggression is associated with the thermal quality of an individuals' habitat, with variation in average daily temperature during the mating season across our site resulting in spatial variation of individual aggressive phenotypes. We also demonstrated that environmental variation (i.e.

variation in the percentage of rock cover in an individual's territory), and individual aggression, influences male reproductive success and female reproductive output. This study represents a first step in disentangling the complex relationships between environmental variation and individual behavioural variation in determining fitness and (potentially) population dynamics. Further work manipulating both environmental characteristics and the spatial mix of behavioural phenotypes within populations will be important in fully elucidating these relationships. Furthermore, examining other aspects of fitness (e.g. within versus extra pair paternity, growth, survival of offspring), population processes (such as dispersal) and habitat quality (such as insect abundance) will be essential in determining how these factors may work together to affect eco-evolutionary dynamics.

Ethical Note

All research was carried out under the requirements of the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th edition, 2004 and the University of Tasmania Animal Ethics Guidelines. All work was carried out under the University of Tasmania Animal Ethics Permit A0010061 and the Tasmanian Department of Primary Industries, Parks, Water and the Environment Permit FA 08245. All individuals were released at the exact point of capture following field measurements, laboratory aggression assays or birth.

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Chapter Eight

General Discussion

Increasingly, we are coming to understand that personality traits are important for, and have an influence on, a range of individual life history processes. These personality based differences will in turn influence population dynamics, community dynamics, eco-evolutionary processes and evolutionary trajectories. While potential proximate mechanisms underpinning intra-individual consistency and inter-individual variation in personality traits, and the influence these personality traits have on ecological and evolutionary processes have been identified, few studies have considered both proximate mechanisms and ultimate outcomes within the same population (but see for exceptions, work on great tits, *Parus major*, by van Oers and Naguib 2013, stickleback fish, *Gasterosteus aculeatus*, by Bell et al. 2013 and primates by Weiss and Adams 2013).

This thesis stemmed from a long-term on-going field project examining population dynamics in *Egernia whitii*, a social Australian skink species. Previous work in the *Egernia* system has demonstrated that individuals display consistent intra-individual differences in aggression, and that female aggression is important for both mode of paternity acquisition (within versus extra-pair paternity) and offspring survival (see Sinn et al. 2008 and While et al. 2009a). Based on these findings and the known importance of personality traits in a variety of other systems, I took an integrated approach to examine personality in this well characterized free-living population of *E. whitii* (see Figure 1). Through conducting this project, I aimed to gain a greater understanding of how personality influences population and ecological dynamics within a free-living population, the mechanism(s) that underpin personality, and the way in which personality may ultimately shape evolutionary trajectories of populations. Below, I integrate and synthesize my work presented in the disparate chapters and summarize how this work contributes to our understanding of the potential role of personality in evolutionary ecology.

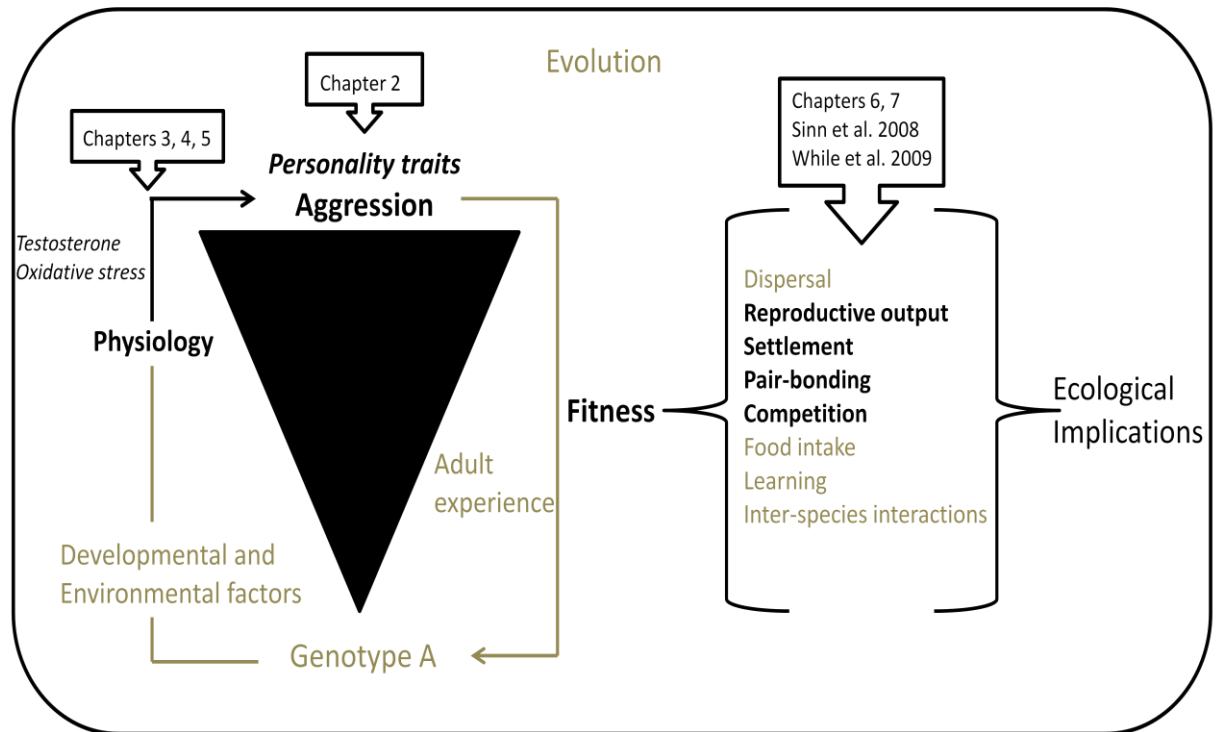


Figure 1: Revisited conceptual diagram from Chapter One. This diagram conceptually demonstrates the proximate underpinnings and the ecological role of personality. How the work contained in this thesis adds to our knowledge of these processes is indicated in bold, with previous work on female *E. whitii* also included (female reproductive output and social strategy (indicated by ‘pair-bonding’). While I initially examined overall personality (five key personality traits, as indicated by ‘personality’ in bold italics) in both sexes (Chapter 2), I focused the majority of this work on aggression in male *E. whitii*.

Aggression as a key personality trait in *Egernia whitii*

Individuals of the same species differ in what they do, which has long been recognized by observers of the natural world (Aristotle 350 BCE, Darwin 1859, see also Bell 2007, Dall et al. 2012). However, despite the potential for behaviours to be very flexible, individuals often display limited behavioural plasticity; they appear to be somewhat constrained in their behavioural response and instead display consistent intra-individual differences in behaviour. These consistent intra-individual differences in behaviour (i.e. personality traits), have become an increasing focus of research over the last decade (Sih et al. 2004a, b, Carere and Eens 2005, Bell 2007, Duckworth 2010, Réale et al. 2010a, Stamps and Groothuis 2010a, b, Dall et al. 2012, Wolf and Weissing 2012). Personality has important implications for evolution as

personality traits which are correlated with each other do not evolve in isolation, but rather as a package, and this can generate trade-offs and canalizing effects which define boundaries to unlimited plasticity (Carere and Eens 2005, Duckworth 2009). Researchers have also suggested that the study of animal personality allows, and in fact requires, an interdisciplinary approach that integrates proximate mechanisms with ecology and evolution (Sih et al. 2004a, b, Carere and Eens 2005). Sih et al. (2004a, b) therefore argued that the study of animal personality represents a conceptual shift in how we view and study behaviour and its integration with ecology and evolution.

The first step in studying animal personality is identifying and characterizing personality traits relevant to your study system (Bell 2007). In order to identify traits of interest in my study system, I followed the suggestion outlined in Réale et al.'s (2007) paper on integrating personality with ecology and evolution, that there are five common personality traits which relate to separate ecological contexts, are potentially common across a range of species, and are key targets of selection. These five personality traits – aggression, exploration, boldness, activity and sociability – have been demonstrated as being associated with important life history traits and fitness outcomes, such as the positive association between boldness and reproductive success (Smith and Blumstein 2008, Réale et al. 2010a). Inter-trait correlations (i.e. behavioural syndromes) have also been demonstrated with the most common being a positive link between exploration, boldness and activity (Réale et al. 2007, Sih et al. 2012). Two of the key questions in the field of animal personality is whether behaviours are always related to each other in the same way, and whether relationships between behaviours and behavioural correlations are different between groups (groups being sexes, age cohorts, populations or species; Bell 2005, Bell 2007, Stamps and Groothuis 2010a).

In adult *E. whitii*, aggression has previously been demonstrated to be a consistent personality trait. Individuals retain their aggressive rank (relative to others in the population) over a period of months (Sinn et al. 2008, While et al. 2009a). My research has confirmed that over a period of months, and up to a year, aggression is a consistent and structurally stable personality trait in adults of this species (Chapters 2-

7). Remarkably, across the six years of study for which we have individual aggression information, aggression remains highly consistent ($F_{(7,35)} = 7.044$, $\rho = 0.858$, $p < 0.0001$). *Egernia* reach sexual maturity at approximately three years, and live for approximately 10 years (Chapple 2003). This multi-year consistency therefore implies lifetime consistency in this trait. Lifetime consistency estimates of personality traits are rare in nonhuman animals (see Sinn et al. 2008 for lifetime personality estimates in dumpling squid *Euprymna tasmanica* and Magnhagen et al. 2012 for a study on long-term boldness in perch *Perca fluviatilis*). Additionally, aggression consistency estimates in *E. whitii* are generally well above the reported average of repeatability in the expression of aggression at $\rho = 0.5$ (see meta-analysis by Bell et al. 2009). High repeatability indicates both low within-individual variance over time, as well as high among-individual variance (Boake 1989, Bell et al. 2009). In other words, individuals are behaving in the same manner across time, and differ from each other. High repeatability of a trait, especially over a lifetime, indicates that the expression of the behaviour is canalized or under strong proximate (i.e. physiological) constraint (Castellano et al. 2002, Smith and Hunter 2005, Bell et al. 2009, see also Andrew 1972 and Wingfield 1994 on the persistence of aggression), is not state-dependent (Dingemanse and Wolf 2010, Luttbeg and Sih 2010, Wolf and Weissing 2010), that there is an advantage to behaving consistently, consistency is selected for (Dall et al. 2004, McElreath and Strimling 2006, Nakagawa et al. 2007, Schuett et al. 2010) and that there may be a heritable component to the trait (Boake 1989).

In contrast, I found limited intra-individual consistency for boldness, activity, exploration and sociability (see Figure 1, Chapter 2- McEvoy et al. in review). The variability that I found in the structural and intra-individual consistency in these traits, combined with variable inter-trait correlations, highlights two points. Firstly, that measuring personality and inter-trait correlations is not straightforward and careful consideration should be given to the measurement and description of personality traits (see also Réale et al. 2007, Biro and Stamps 2008, Dingemanse et al. 2010). Secondly, this study, in conjunction with previous work on *E. whitii* (Sinn et al. 2008, While et al. 2009a), confirms that aggression is a structurally stable, highly consistent trait in this species, while the other measured personality traits are

not. The structural and temporal consistency of aggression allows us to ask questions about both the proximate mechanisms underpinning and perhaps constraining this trait, as well as the ecological importance of, and selection on, the trait (within this species). The rest of this thesis focused on elucidating the proximate mechanisms that may underpin consistency in aggression in this species, and the functional ecological significance of the trait to adult *E. whitii*.

The proximate mechanisms governing aggression

There is a long history of study regarding the relationships between aggression and the steroid hormone testosterone (Wingfield et al. 1987, Marler and Moore 1988, 1989, Wingfield et al. 1990, Groothuis et al. 2005, Kempenaers et al. 2008), and the endocrine system has been suggested as a key proximate mechanism that organizes and maintains personality traits (Sih et al. 2004a, b, Koolhaas et al. 1999, Baugh et al. 2012). The logical step was therefore to examine the relationship between testosterone and aggression in this species. In the majority of vertebrate species, testosterone is known to be associated with aggression, with higher levels of circulating plasma testosterone generally linked to higher levels of aggression, particularly in males (Wingfield et al. 1987, 1990, Strasser and Schwabl 2004, Müller et al. 2008). However, the relationship between aggression and testosterone is not as straightforward as previously assumed (Adkins-Regan 2005, Ball and Balthazart 2008, Apfelbeck and Goymann 2011, Cramer 2012, Duckworth and Sockman 2012). A number of avian species aggressively defend territories even when plasma testosterone concentrations are low, and in some cases, aggression and testosterone are unrelated, or negatively related (see Chapter 4- McEvoy et al. in review). The relationship between testosterone and aggression in male *E. whitii* confirms this complicated relationship, with negative correlations found between aggression and baseline testosterone concentrations as well as during up-regulation of testosterone following a conspecific aggression challenge (Chapter 3- While et al. 2010 and Chapter 4- McEvoy et al. in review). Testosterone and aggression are unlinked in female *E. whitii* (Chapter 3- While et al. 2010). These results are the first to demonstrate that plasma testosterone concentrations and aggressive behavior are *negatively* related both at the baseline level as well as during the up-regulation of testosterone directly after an aggressive interaction. Additional work exploring the

complicated endocrine pathways through which aggression may be mediated in this system is needed in order to fully elucidate this relationship.

While this work adds to our knowledge of both the interplay between testosterone and aggression, and a proximate physiological factor that may be responsible for maintaining personality traits, it is not conclusive. A number of additional proximate factors should also be considered. The high level of repeatability that we see in aggression in this species (all chapters, plus Sinn et al. 2008 and While et al. 2009a) suggests a strong heritability component to this trait (Boake 1989). While there might be a genetic basis to personality (Dochterman and Roff 2010, Stamps and Groothuis 2010b, van Oers and Sinn 2011), genes, being structural biochemical units, can only be expressed in behaviour through a translational process involving interaction with other genes and further internal and external factors. Behaviour is an end-product of this process of continuous interaction (Groothuis and Trillmich 2011). The developmental environment that an individual experiences may therefore be a key factor that shapes an individual's personality. In *Egernia*, a long-lived species which do not mature until approximately three years of age (Chapple 2003, While et al. 2009a, b, c, 2011), studying the development of personality throughout ontogeny was beyond the scope of this PhD. However, previous work has shown that early life developmental conditions influence survival and growth in juvenile *E. whitii* over the first two years of life (Appendix 1: While et al. 2009). This suggests that conditions experienced during ontogeny can influence the development of phenotypes, potentially including personality. A number of recent review papers have advocated the importance of considering developmental factors in shaping personality and the necessity to study individuals throughout ontogeny (see Stamps and Groothuis 2010a, b, Groothuis and Trillmich 2011). These reviews argue that genes and experiential factors interact throughout ontogeny to affect the expression of personality traits (Stamps and Groothuis 2010a) and that studying personality development through ontogeny is crucial for understanding the proximate and ultimate aspects of personality (Groothuis and Trillmich 2011).

Metabolic rate has recently been proposed as a mechanism by which consistent individual differences in behaviours may be maintained (Biro and Stamps 2008,

Careau et al. 2008, Biro and Stamps 2010). This is because energy, and the acquisition and processing of energy, are essential to fuel all the processes of the body (Biro and Stamps 2010). Personality traits can be energy gaining, or energy expensive. For example, foraging will induce a net energy gain over time, while aggression will result in an energy loss as aggression requires increased activity (Marler et al. 1995, Ros et al. 2004, Costantini et al. 2008, Biro and Stamps 2010). Any behavioural trait with an energy cost sustained over time, such as the consistent intra-individual aggression seen in *E. whitii*, should therefore be positively associated with metabolic rate (Biro and Stamps, 2010). While we did not measure metabolic rate directly, we did measure aspects of oxidative stress which is a consequence of metabolism (Chapter 5- Isaksson et al. 2011). Although there was no association between aggression and our measured aspects of the oxidative stress system in females, there was a positive association between aggression and antioxidant capacity in males. This suggests that in males aggression may induce an increased oxidative challenge resulting in an elevation of antioxidant defence. While these results need to be verified experimentally (see also Metcalfe and Monaghan 2013), they do suggest that examining metabolic rate as a proximate mechanism for maintaining consistent intra-individual differences may be a promising area of research (echoing suggestions by Biro and Stamps (2008) and (2010) and Careau and colleagues (2008)).

Ecological implications of aggression

Given that we find a potential cost to aggression, and such strong intra-individual consistency in aggression (all chapters plus Sinn et al. 2008 and While et al. 2009a) what is the ecological significance of aggression in this species? My research, combined with previous research has demonstrated that there are clear ecological implications to aggression in female *E. whitii* (Chapter 7, Sinn et al. 2008, While et al. 2009a). More aggressive females have a higher reproductive effort, more aggressive females more likely to have extra-pair (vs. within-pair) offspring, and offspring born to more aggressive mothers are more likely to survive over winter (Chapter 7, Sinn et al. 2008 and While et al. 2009a). However, the ecological role of aggression in males was not investigated in these studies. A key life history trait in which aggression is likely to be important to males is intra-sexual competition. Males compete for access to a variety of resources, and more successful males in

competitive encounters are likely to reap rewards, including increased mating opportunity (Huyghe et al. 2005; Arnott and Elwood 2009). However, in examining both direct competition (through a laboratory experiment), and the key outcomes of competition in the field (reproductive output and male/female overlap of territories), there was no indication that aggression was an important contributor to a successful outcome (Chapter 6- McEvoy et al. 2013). However, given the strong consistency of aggression in males (Chapters 2-7), and the well-established costs associated with aggression (Lincoln et al. 1972, Wingfield et al. 1987, Constantini et al. 2008, Logue et al. 2011), including those established in *Egernia* (Chapple 2003, Langkilde and Shine 2004, 2007, Langkilde et al. 2005, Chapters 3-6), it is unlikely that aggression is a selectively neutral trait.

Further investigation revealed that aggression may be important for male competitive ability but in a context-dependent manner (Chapter 7). Specifically, the importance of aggression for competitive ability appears to be dependent on resource availability. When high-quality resources in the environment are limited, aggression appears to be important to males in securing those resources to influence reproductive output (see also Johnson and Sih 2005). In resource-limited areas, more aggressive males produced more offspring; however, in resource-abundant areas, aggression did not appear to influence reproductive output. Research in other species has demonstrated that fluctuating selection pressures related to environmental variation are responsible for maintaining variation in personality traits (e.g. Dingemanse et al. 2004). Although the resource in the *Egernia* system does not fluctuate in a temporal manner, it does vary spatially, and competition for the benefits associated with these resource rich areas may influence the importance of aggression (see also Johnson and Sih 2005). In resource-limited areas, aggression will be important to secure what resources there are, and this will be reflected in a male's reproductive output. Females are likely to be attracted to mates that hold high quality territories, or be attracted to these resource-abundant areas themselves, and density in these areas is likely be higher (Barley and Coleman 2010, Geange and Stier 2010). This would decrease the importance of aggression *per se* in male reproductive success in these areas (see also discussion in Chapter 7).

Conclusions

Consistent intra-individual differences in behaviour are an important dimension of ecologically and evolutionary relevant intra-specific variation (Réale et al. 2010b, Dall et al. 2012, Wolf and Weissing 2012). Wolf and Weissing (2012) pointed out the different ways in which personality can enhance and inform our understanding of ecological and evolutionary processes; below I demonstrate the ways in which my results fit into their framework.

First, the highly structured nature of personality traits (e.g. aggression in this study: see Chapter 2; but also Chapters 3-7) implies constrained behavioural plasticity which can trigger ecological and evolutionary consequences not expected in the presence of less structured variation (e.g. survival and reproductive output associated with personality; see Wolf and Weissing 2012). Differences in personality traits have been systematically demonstrated as being associated with differences in life history traits (Chapter 7, see also Smith and Blumstein 2008 review), and are thought to be selected for as part of a pace-of-life syndrome (e.g. Réale et al. 2010b, Careau and Garland 2012, and Chapters 2 - 5 in which aggression is shown to be associated with physiological aspects of this syndrome) which further reinforce life-history differences. Life history parameters are key determinants of individual fitness, and by extension, population demographic parameters (Wolf and Weissing 2012). These parameters directly affect population growth (see Le Galliard 2005, Mougeot et al. 2003, 2005) which can lead to ecological and evolutionary change (e.g. Mougeot et al. 2003, Duckworth 2006, Duckworth and Badyaev 2007).

Second, personality traits that result in non-random distribution of phenotypes in the environment affect the interaction dynamics of phenotypes which may have substantial ecological and evolutionary consequences. In *E. whitii*, there appears to be a non-random spatial distribution of aggression phenotypes related to temperature (more aggressive individuals found in warmer areas: see Chapter 7; see also Duckworth 2006). This spatial segregation can cause cascading effects throughout the ecosystem. It can enhance differences between personality phenotypes due to differing selection regimes associated with micro-environmental differences. This results in individuals experiencing differences in resources, predators and pathogens

(Wolf and Weissing 2012; see also studies on bluegill sunfish *Lepomis macrochirus* by Werner et al. 1981, Wilson 1998, Neff et al. 2003, Sih et al. 2003, Wilson et al 2011; and theoretical work by Nowack et al. 2010). Spatial segregation can also influence intra- and inter- species competition, which can further influence other aspects of an individual's phenotype, such as physiology (see Chapter 4 for an aggressive interaction influencing a physiological response).

Third, personality differences encourage individual differences in other ecologically and evolutionarily relevant traits/processes (Wolf and Weissing 2012). For example, consistent individual differences result in life history differences, such as the interaction between aggression and habitat in influencing reproductive output in male *E. whittii* (see Chapter 7 and associated discussion; see also Chapter 7, Sinn et al. 2008 and While et al. 2009a for habitat and female aggression influencing reproductive effort, and female aggression influencing offspring survival and paternity acquisition). Personality can also be associated with physiology, such as the association between testosterone and aggression (Chapter 3 and 4) and parameters of oxidative stress (Chapter 5) seen in this study which can further influence other aspects of an individual's phenotype and life history processes (e.g. testosterone influencing parental care, e.g. McGlothlin et al. 2007, and oxidative stress influencing senescence e.g. Beckman and Ames 1998).

Fourth, personality can be important at both ecological and evolutionary timescales as personality differences can affect the stability, resilience and persistence of populations, communities and whole ecosystems (Réale et al. 2010b, Dall et al. 2012, Sih et al. 2012, Wolf and Weissing 2012). A population harboring individuals which vary in their personality traits (such as variation in aggression seen in *E. whittii*) is expected to exhibit less density fluctuations around the population equilibrium and be less vulnerable to environmental change (Wolf and Weissing 2012). Different personality types react differently to environmental change resulting in a less extreme response to, and an ability to better cope with, novel conditions as a whole (i.e. a buffering affect at a population level) (Wolf and Weissing 2012).

My research, combined with Sinn et al. 2008 and While et al. 2009a, indicates that the aggression personality trait in *E. whitii* will have consequences for ecological and evolutionary dynamics. Aggression in this species mediates social interaction structures, spatial distribution and resource exploitation patterns (see also Wolf and Weissing 2012). Aggression determines (at least in part) the environment of individual *E. whitii* which will result in different selection regimes acting on individuals (see also Duckworth 2009). Aggression in this species is linked to non-behavioural phenotypic variation (i.e. physiology), perhaps as a result of reciprocal correlation involving reinforcing feedback loops between behavioural and non-behavioural traits (Dall et al. 2004, Sih and Bell 2008, Wolf and Weissing 2012). Combined, this indicates a phenotype in which aggression plays a central role in mediating an individuals' environment and subsequent selection pressures and in which a behavioural (i.e. aggressive) response will be a key aspect of how individuals respond to change (Duckworth 2009). While further manipulative work is needed to fully elucidate the consequences of both proximate mechanisms underpinning aggression and the eco-evolutionary dynamics of aggression in this species, this thesis provides a vital initial step in a holistic examination of the role of aggression as a key personality trait in a free-living vertebrate population.

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Appendix One

Long-lasting effects of among- but not within-litter timing of birth in a viviparous lizard

Abstract

Background: Early developmental conditions can influence within and among brood variation in the timing of hatching/birth, which has been shown to affect offspring survival, growth, and reproductive success across a range of species.

Problem: How does within and among litter variation in the timing of birth affect offspring growth and survival in *E. whitii*?

Organism: *Egernia whitii*, a long-lived social reptile which exhibits within litter variation in its timing of birth (i.e., birthing asynchrony).

Methods: We measured offspring growth and survival in a natural population of *E. whitii* by following three cohorts of offspring from birth to their second year of life (the year before the onset of reproduction).

Conclusions: (1) Year of birth is the strongest predictor of offspring survival over the first two years of life. (2) The effects of year of birth on offspring survival over the second year of life are independent of its effects over the first. (3) Within year date of birth is the strongest predictor of offspring growth over the first two years of life, with offspring born early in the year having greater growth over their first two years of life than offspring born later in the year. (4) Examining only growth over the second year of life (i.e., controlling for growth over the first year), removed the effect of date of birth on offspring growth. (5) There are no effects of within litter timing of birth (i.e., birthing asynchrony) on offspring growth or survival.

Introduction

Early environment conditions can have both short- and long-term consequences for individual fitness. Such conditions frequently involve maternal effects (Mousseau and Fox, 1998; Uller, 2008). In ecological settings, this has been most extensively studied in birds, where both within and among brood variation in developmental conditions, in particular the timing of hatching, has been shown to affect offspring growth, survival, and reproductive success (summarised in Lindström, 1999). Generally, offspring from later broods frequently have lower survival than offspring from earlier broods and this effect may last past fledgling (Perrins, 1967; Sheldon et al., 2003). Timing of hatching within broods (i.e., hatching asynchrony) can also have significant effects on offspring phenotype and fitness (see Stoleson and Beissinger, 1995 for a comprehensive review). In particular, the degree of hatch spread and an individual's hatching position can mediate offspring competitive ability and competition levels within the brood, which themselves influence offspring growth and survival (e.g., Badyaev et al., 2002; Johnson et al., 2003; Stienen and Brenninkmeijer, 2006). However, while the short-term consequences of hatching asynchrony are well documented and frequently strong, the long-term consequences have been less well studied, despite that it may be important for understanding selection on hatching asynchrony (Mock and Forbes, 1994).

Short- and long-term effects of the timing of hatching or birth remain less studied in reptiles. However, recent research has identified consistent, and in some cases long-lasting, effects of between litter variation in hatch/birth date across a range of squamate reptiles (Olsson and Shine, 1997; Madsen and Shine, 2000; Qualls and Shine, 2000; Wapstra, 2000; Warner and Shine, 2005; Warner and Shine, 2007). In contrast, differences in within-litter timing of hatching or birth are virtually absent as individual females typically lay their eggs, or give birth, synchronously (Norris, 1997, but see Radder and Shine, 2007). The viviparous lizard genus *Egernia* diverges from this pattern. Although embryo development within litters is synchronous birth is spread over several days (i.e., birthing asynchrony; While et al., 2007). This within litter variation in the timing of birth is analogous to hatching asynchrony in birds and results in the creation of sibling size hierarchies that influence offspring growth and survival (While and Wapstra, 2008; While and Wapstra 2009). In birds, the order of

hatching is the primary mechanism governing the development of sibling hierarchies, and thus offspring size and survival, with first hatched offspring gaining an advantage over later hatching offspring through increased opportunity for growth and increased competitive ability (e.g. Badyaev et al., 2002; Johnson et al., 2003; Stienen and Brenninkmeijer, 2006). In contrast, short-term studies have failed to identify any effect of birth order on offspring size (both relative and absolute) or survival within *Egernia* (While and Wapstra, 2008). However, the long-term effects of birthing asynchrony are yet to be examined in natural populations. As the consequences of birthing asynchrony in the wild may be reliant on parameters unable to be replicated within the laboratory (e.g., the opportunity to disperse, the use of parental home ranges, or the level of conspecific competition), examining the long-term effects of birthing asynchrony within a natural setting may give us valuable insights into the factors responsible for the evolution and maintenance of birthing asynchrony within this genus.

The aim of this study was to examine how within and between litter variation in the timing of birth affects offspring growth and survival within *Egernia whitii*, by following three cohorts of offspring from birth to their second year of life, i.e., the year before the onset of reproduction (Chapple, 2005).

Materials and Methods

Study Species

White's skink (*Egernia whitii*) is a medium sized (up to 100mm snout-vent length) viviparous lizard found throughout southeastern Australia. Our study population is located at Orford, on the East Coast of Tasmania, Australia (42°57'S, 147°88'E). Males and females are sexually monomorphic, become reproductively mature at approximately 3 years, and display an overall lifespan of 9 – 10 years (Chapple, 2003). Reproduction is annual, with mating typically occurring during the spring (Sep to Oct) and gestation spanning 3 - 4 months (While et al., 2007; While et al., 2009a). Birthing asynchrony has previously been documented in this population, occurring in 100% of litters (While et al., 2007). In the field females give birth to offspring with an average of two days between births (range 1 – 10), which, under experimental conditions, results in formation of size hierarchies (While and Wapstra, 2008; While

and Wapstra 2009). However, spread of births varies between litters within years and in the mean spread between years (While et al., 2007).

Field and laboratory data collection

We conducted the field study during the lizards activity season (Aug to Apr) over three consecutive years (2005 to 2007), with the methodology identical for all three field years (see also While et al., 2007; While et al., 2009a; While et al., 2009b; for detailed description of the field site and field and laboratory methodology). At the beginning of each season, all individuals in the population were (re)captured, measured for weight (± 0.1 mg) and length (snout-vent and total length ± 0.5 mm), and had their sex determined via eversion of the hemipenes. At the end of gestation (mid Jan), all gravid females were caught and returned to the University of Tasmania, Hobart, Australia, to give birth. Females were housed individually in rectangular plastic terraria (300 x 600 x 400 mm), in temperature- and light-controlled rooms with lights set to ambient day lengths (Hobart, Tasmania, Australia). Housing terraria contained a basking rock and basking light at one end and a shelter at the opposite end. This provided a thermal gradient of 40 °C to 17 °C in the terraria, allowing females to actively thermoregulate. Food (*Tenebrio* larvae, crushed fruit) and water were available *ad libitum*. Basking lights were set on a timer to come on 1 hour after room lights were turned on and to turn off 1 hour before room lights went off. During the period of offspring birth, cages were checked twice daily for offspring. At birth, offspring were temporarily removed from their mother in order to be marked, weighed (± 1 mg), measured for snout-vent length, and total length (± 1 mm). Offspring condition was then calculated by regressing offspring mass over its snout-vent length. We were unable to identify sex of offspring as juvenile female *Egernia* retain their hemipenes (Chapple, 2003). In addition to offspring morphometrics, birthing asynchrony characteristics, including birth order and spread between births within a litter, were also recorded. Within 3 days of the birth of the final offspring, offspring were released, with their mother, at their mothers' site of capture.

During each subsequent field year we recaptured all surviving offspring at the study site, recording date of recapture and morphometric traits (weight, ± 1 mg; snout-vent and total length, ± 1 mm), allowing us to estimate offspring growth and survival (total

observations per year = 1866 ± 126). As the study site is flanked on all sides by physical barriers (e.g. roads and unsuitable habitat), emigration into the site by unmarked individuals is low, and captures of marked animals outside the study area is low (< 10 observations per year), estimates of offspring survival are highly unlikely to be compromised by dispersal of offspring out of the study site. Furthermore, only two offspring were recaptured following their second year that had not been recaptured during their first, suggesting a high level of accuracy in our recapture methods.

Statistical analysis

Differences in female reproductive characteristics (clutch size and birth date) and offspring morphometrics (condition and snout-vent length) at birth as a function of year of birth and birth date were analysed using general linear mixed models (PROC MIXED in SAS STAT v.9.2). For all models year of birth was entered as a fixed factor, date of birth (calculated as the number of days from the 1st of January each year) as a co-variate, and female id as a random factor. The effect of among- and within-litter timing of birth on offspring growth and survival over their first two years of growth was analysed using general linear and generalized linear models (PROC GLM and PROC GENMOD respectively). For both sets of models, offspring growth (calculated as svl at capture – svl at birth) or survival were entered as the dependent variable, season and birth order (1, 2, or 3) were entered as fixed factors, and date of birth, date of recapture (both calculated as the number of days from the 1st of January each year), and snout-vent length were entered as covariates. For the logistic survival models, date of recapture was not included in the model as only surviving offspring had a date of recapture. We did not include litter identity as a random factor within the growth and survival models because the majority of litters (72%) only had one offspring surviving into subsequent years and thus we had relatively low statistical power to control for litter identification. For linear models, post hoc tests were carried out using a Ryan-Elliot-Garbriel-Walsh multiple range test. All models started with the full model including all interaction terms and we subsequently eliminated non-significant interaction terms backward, starting with higher order interaction terms, at p-values > 0.25 (Quinn and Keogh, 2002). We report here results for models containing all main effects following backward elimination. Where mixed models

were used, significance of fixed effects was tested using F-tests, with the degrees of freedom calculated using the Satterthwaite's approximation (Littell et al., 1996). All data were checked for violations of assumptions, including homogeneity of slopes where covariates were used. Means \pm 1 standard error (SE) are reported throughout.

Results

Ninety-one females were brought into the laboratory to give birth over the 3-year field study. These females gave birth to a total of 182 offspring, with an average litter size of 2.03 ± 0.07 . Date of birth differed between years, with females in 2006 giving birth later in the year than females in 2005 or 2007 ($F_{2,162} = 6.87$, $P < 0.01$; Figure 1). There were no differences in female litter sizes between years ($F_{2,59.41} = 0.84$, $P = 0.44$), nor did offspring size (svl) differ between ($F_{2,178} = 1.44$, $P = 0.24$) or within years ($F_{1,178} = 0.73$, $P = 0.39$). However, within years, there was a weak relationship between birth date and offspring condition ($F_{1,118} = 3.95$, $r^2 = 0.03$, $P = 0.05$), with offspring born later in the year in poorer condition at birth than offspring born earlier in the year.

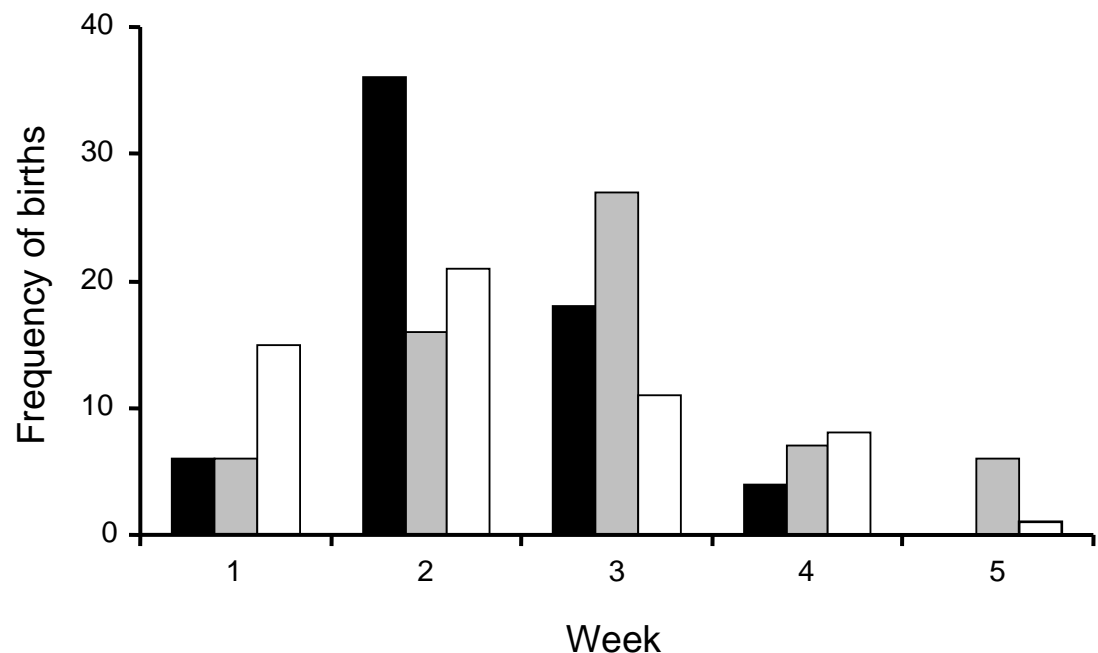


Figure 1. Frequency of births for female *Egernia whitii* held under natural conditions in 2005 (■, n = 64 births), 2006 (■, n = 62 births), and 2007 (□, n = 56 births). Week 1 begins the 15th of January each year and Week 5 begins the 12th of February.

Offspring exhibited relatively high survival over their first year, with 70 of the 181 offspring released with their mothers surviving, representing a survival rate of 38%. Of these offspring, 39 also survived over their second year, representing a survival rate of 54% between their first and second years and a total survival rate of 21% over both years. The most significant predictor of an offspring's survival was its year of birth, with offspring born in 2006 having lower survival, across both years of growth, than offspring born in 2005 or 2007 (Table 1; Figure 2), although this effect failed to reach statistical significance over the first year of growth (Table 1). Importantly, the effects of year of birth on offspring survival across the second year of growth were independent of survival across the first. This was evident when we analysed offspring survival across only the second year (i.e., including only offspring that survived their first year) and year of birth remained significant ($\chi^2 = 8.37$, $P = 0.01$). These results suggest long lasting year of birth effects on offspring survival. Neither offspring date of birth, birth order position, nor offspring size at birth predicted its survival across either the first or second year (Table 1).

Table 1. Factors contributing to variation in offspring survival over their first and first two years within a natural population of *Egernia whitii*. [Interaction terms which did not alter the results of the main effects (i.e., p-values greater than 0.25) are not shown, values in bold face represent statistically significant effects].

Years	Predictor Variables	Offspring Survival	
0 - 1 year	Year of Birth	$\chi^2 = 5.40$	P = 0.06
	Birth Order	$\chi^2 = 2.56$	P = 0.27
	Birth Date	$\chi^2 = 0.04$	P = 0.83
	SVL at Birth	$\chi^2 = 0.84$	P = 0.36
0 - 2 year	Year of Birth	$\chi^2 = 12.84$	P < 0.01
	Birth Order	$\chi^2 = 5.05$	P = 0.08
	Year x Birth Order	$\chi^2 = 8.56$	P = 0.07
	Birth Date	$\chi^2 = 0.06$	P = 0.81
	SVL at Birth	$\chi^2 = 0.72$	P = 0.40

We were able to calculate growth across these time periods for the 72 offspring that survived over their first winter and the 39 offspring that survived over both winters. As with survival, we found that there were strong year of birth effects on offspring growth across an individual's first two years (Table 2), with offspring born in 2006 having significantly lower growth than offspring born in either 2005 or 2007 (Figure 3). We also found significant within year timing of birth effects, with a strong relationship between offspring date of birth and offspring growth (Table 2, Figure 4a). Specifically, offspring born early in the year had greater growth compared to offspring born late in the year. These effects held when we re-ran models while controlling for differences in offspring condition at birth, suggesting that the effects of birth date on offspring growth were not influenced by the poorer condition of offspring born later in the season. These effects of birth date on offspring growth lasted into an offspring's second year of growth, although they became substantially weaker (Table 2, Figure 4b). However, examining growth between the first and second years independently (i.e., controlling for snout-vent length growth over the first year), removed the significance of both between and within year effects on offspring growth (year of birth, $F_{2,29} = 2.36$, $P = 0.12$; date of birth, $F_{1,29} = 3.29$, $P = 0.08$). Thus, the effects of year of birth and birth date into the second year of growth were driven by their effects on offspring growth over the first year, in contrast to the effects of birth date on survival. There were no differences in growth between offspring born at different birth order positions over the first two years of growth, nor was growth influenced by an individual's size at birth (Table 2).

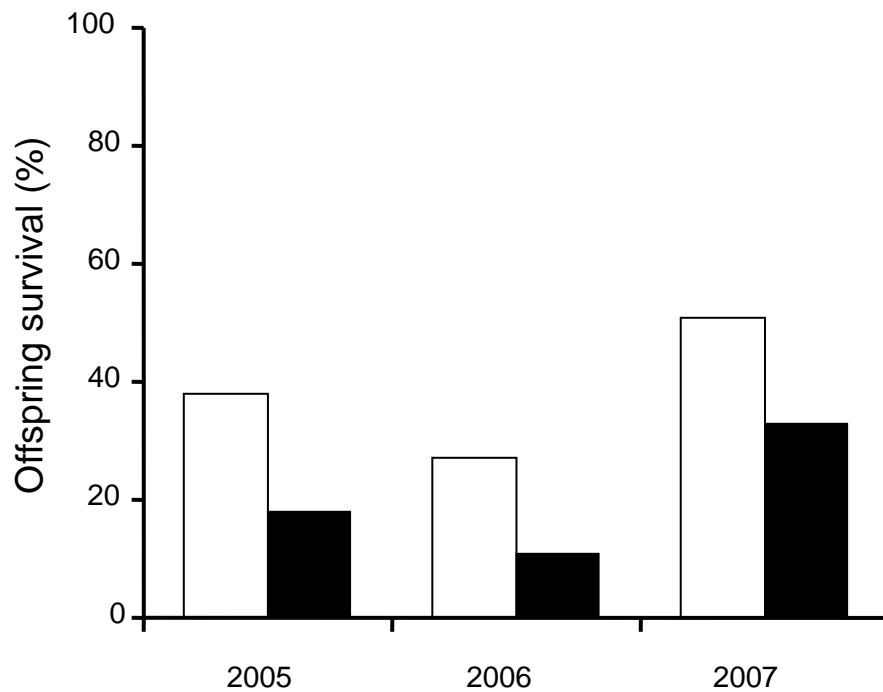


Figure 2. Percentage of *Egernia whitii* offspring born in 2005, 2006, and 2007 surviving across their first year (□) and first two years (■).

Table 2. Factors contributing to variation in offspring growth over their first and first two years within a natural population of *Egernia whitii*. [Interaction terms which did not alter the results of the main effects (i.e., p-values greater than 0.25) are not shown, values in bold face represent statistically significant effects].

Years	Predictor Variables	Offspring Growth (mm)	
0 - 1 year	Year of Birth	F_{2,58} = 7.29	P < 0.01
	Birth Order	F _{2,58} = 8.12	P = 0.37
	Year x Birth Order	F _{4,58} = 1.52	P = 0.21
	Birth Date	F_{1,58} = 35.45	P < 0.0001
	SVL at Birth	F _{1,58} = 0.02	P = 0.80
	Date of Recapture	F_{1,58} = 48.39	P < 0.0001
0 - 2 year	Year of Birth	F_{2,36} = 11.54	P < 0.01
	Birth Order	F _{2,36} = 1.71	P = 0.20
	Birth Date	F_{1,36} = 14.31	P < 0.01
	SVL at Birth	F _{1,36} = 0.48	P = 0.49
	Date of Recapture	F_{1,36} = 21.96	P < 0.0001

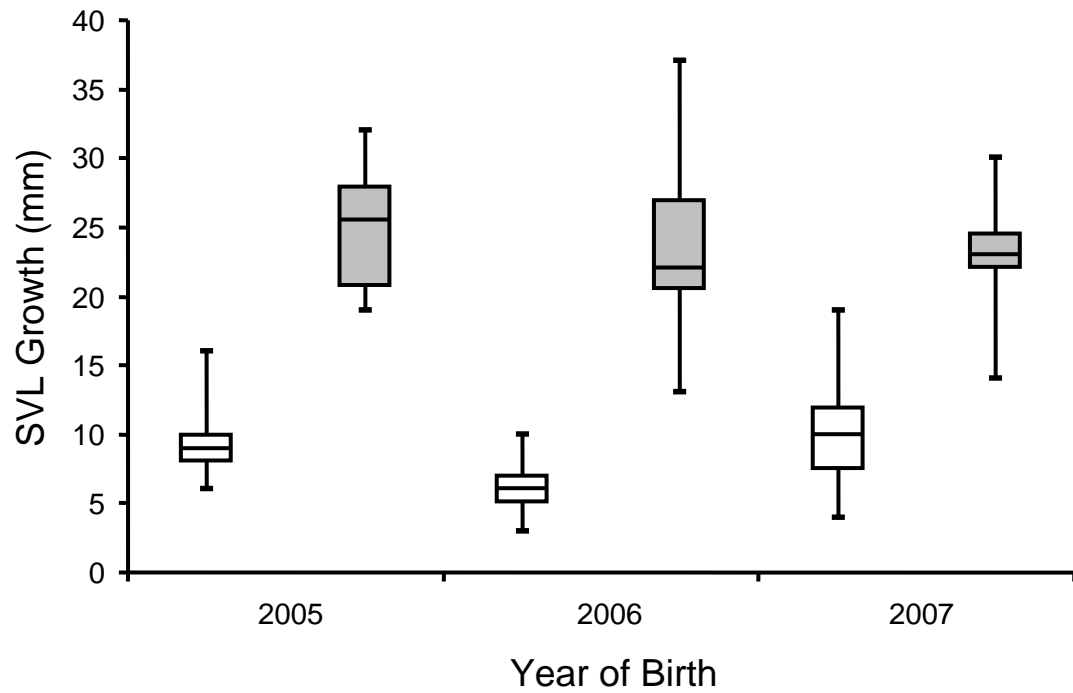


Figure 3. Differences in snout-vent length (svl) growth over the first (□) and first two (■) year of life between *Egernia whitii* offspring born in 2005, 2006, and 2007. The above figure shows median growth (line), the 25% and 75% quartiles (boxes), and the ranges (whiskers).

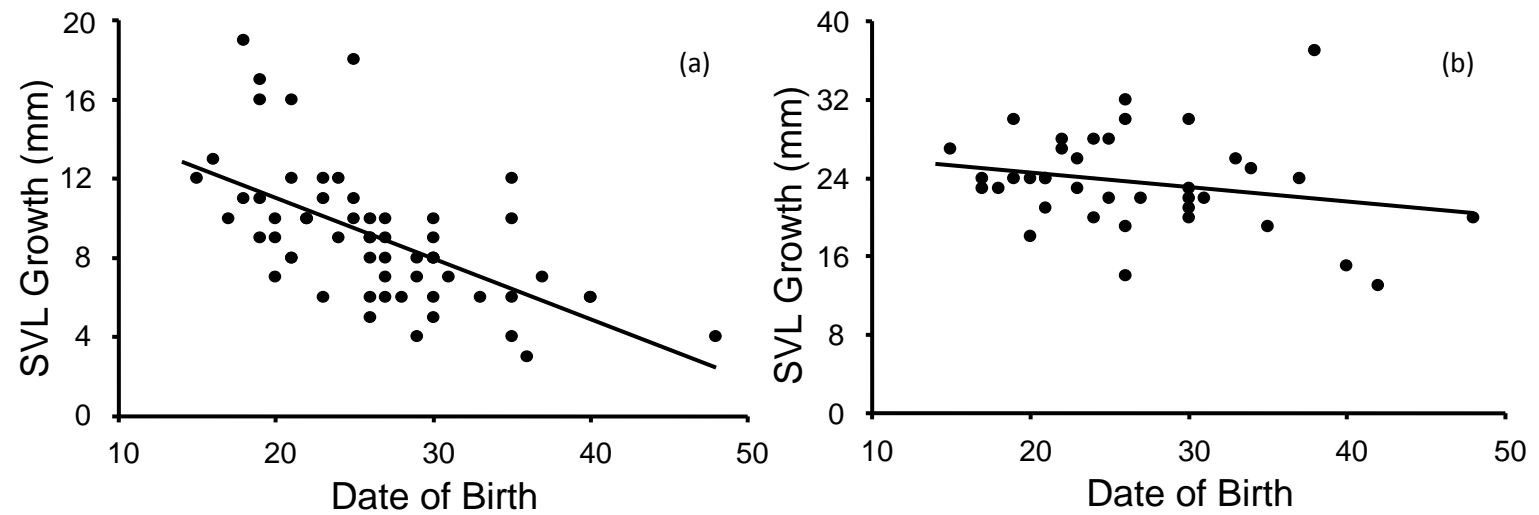


Figure 4. The relationship between snout-vent length growth and date of birth (days from the 1st of January) for *Egernia whitii* offspring after 1 year of growth (a) and 2 years of growth (b).

Discussion

Our data demonstrate strong and long lasting effects of between litter variation in the timing of birth on fitness related traits in a long-lived social reptile. Specifically, we show that between litter timing of birth, both within and between years, is the key predictor of offspring growth and survival. As these effects were both strong and persistent, and may exert a significant influence on key life history traits such as age at maturation (e.g., Warner and Shine, 2007; Warner and Shine, 2008), they suggest strong selection on embryonic development and, as a consequence, female basking behaviour. Conversely, we found no effect of within-litter timing of birth (i.e., birth order) on offspring growth and survival. Thus, the causes and consequences of birthing asynchrony within *Egernia* may differ to those found in some birds where later hatched offspring typically have reduced growth and survival.

Between season effects

Variation in offspring growth and survival across years is expected due to annual variation in climate, demography and resource abundance. Despite this, surprisingly little information exists on inter-annual variation among cohorts in lizards (Olsson and Shine, 1997). Here we show that offspring born in 2006 displayed lower rates of growth as well as lower survival across their first two years of growth than offspring born in the preceding or subsequent years. Importantly, offspring born in 2006 also had reduced survival across their second season of growth independent of survival across their first, suggesting long lasting year of birth effects. Interestingly, the lower survival of offspring born in 2006 over their second year of growth coincided with relatively high survival rates exhibited by offspring born in 2007, who were concurrently experiencing their first year of growth.

These results suggest that conditions early in development, either pre or post-gestation, may result in intrinsic differences in offspring quality that can exert strong influences on an individual's fitness at later life history stages. Such between year 'silverspoon' effects have been described in other vertebrates (Madsen and Shine, 2000; Van de Pol et al., 2006; Descamps et al., 2008), but their ecological and physiological causes are still unknown. In the long-term, between-generation variation in offspring quality, driven by maternal effects, could have important

implications for population demography and both its causes and consequences deserves further study (Colyvan and Ginzburg 2004; Inchausti and Ginzburg et al. 2009). One potential explanation for the long-term effects found in this study is that resource availability at birth may impair development or lead to lasting effects on physiological systems. For example, Madsen and Shine (2000), linked annual variation in cohort growth to variation in prey abundance in a population of water pythons, suggesting that early experience of resource availability can influence energy allocation strategies throughout life. Interestingly, within our population, females who gave birth in 2006 also did so, on average, later in the season than females in previous or subsequent years, suggesting relatively poor thermal conditions during gestation which may have had concomitant effects on offspring quality (Wapstra, 2000). Alternatively, social demographic factors may play a role. *Egernia* display relatively simple social systems typically comprised of stable adult pair-bonds and delayed offspring dispersal (see Chapple, 2003 for a review). However, there is considerable variation in the composition of social groups both within and between populations (Chapple, 2003; While et al., 2009a). For example, we have recently demonstrated yearly variation in parental tolerance of offspring over the same time period, with 2006 having a higher proportion of sub-adults remaining within their parents home range compared to 2005 and 2007 (While et al., 2009a). Thus, competitive interactions between offspring born in that year and their older siblings could suppress growth and potentially increase mortality and/or dispersal out of the home range (resulting in reduced access to resources and protection from conspecific aggression; O'Connor and Shine, 2004; Sinn et al., 2008). Long-lasting effects of sibling interactions have been shown in birds and mammals (Mock and Parker, 1997; see also Uller 2006), but the mechanisms are yet to be elucidated. Nevertheless, social conditions early in life have been shown to mediate hormone levels and responses to environmental conditions later in life (Clark and Galef, 1998; Oddie, 2000; Cushings and Kramer, 2005), both of which could have significant ramifications for growth and survival throughout life.

Within season effects

In addition to strong effects of between-year timing of birth we also showed that variation in within-year timing of birth has a strong influence on offspring growth.

These results are consistent with recent research on lizards that have emphasized the importance of seasonal timing of birth for offspring growth and survival (e.g., Warner and Shine, 2005, 2007). This is in contrast to the general assumption that size, as opposed to birth date, is the key predictor of offspring growth and survival (Forsman 1993; Sorci and Clobert, 1999; Janzen et al., 2000). Indeed, we found that while within year timing of birth significantly influenced offspring growth offspring size at birth had no effect. These effects of birth date on offspring growth are most parsimoniously explained by the shorter growth period before the onset of hibernation for offspring born later in the year (Warner and Shine, 2007; Uller et al., 2007) but could also be driven by variation in maternal/offspring quality or maternal effects linked to birth date (Wapstra, 2000; Uller et al., 2007). For example, mothers whose parturition of offspring is delayed may also invest relatively less into current reproduction or choose relatively cooler basking conditions that have a combined effect on date of parturition and offspring quality (e.g., Wapstra, 2000). We found a significant negative relationship between date of birth and offspring condition at birth across all years, thus offspring growth rate in relation to birth date may be driven by poorer condition at birth rather than their increased opportunity to grow. However, the strong effect of offspring birth date on growth remained when we controlled for offspring condition at birth. Consequently, maternal selection on the timing of birth (i.e., increased basking) may be stronger than resource allocation *per se*. This is perhaps unsurprising as altering female basking frequency and thus parturition date, which can result in a 5mm gain in offspring growth over their first year compared to offspring born later in the season (see Figure 4a), may be relative inexpensive compared to increasing maternal investment itself.

Within litter effects

The main goal of this study was to document the consequences of birthing asynchrony, a phenomenon that seems to be unique to *Egernia* but closely resembles hatching asynchrony in birds (While et al., 2007). However, in contrast to the strong between litter effects, within litter variation in the timing of birth did not influence either offspring growth or survival. These results are in line with previous experimental work that failed to identify strong birth order effects under controlled conditions on either of these traits or on an individual's competitive ability early in

life (While and Wapstra, 2008). As birthing asynchrony is not a result of physiological constraints on the synchronous development of offspring (While et al., 2007), the lack of a birth order effect on growth and survival is surprising and raises questions regarding the adaptive basis of asynchronous birthing within this genus. Birthing asynchrony in *Egernia* is thought to be an adaptation to a highly competitive social environment (While et al., 2007; While and Wapstra, 2008), where the establishment of a size hierarchy promotes dispersal of subordinate offspring and philopatry of dominant offspring, the latter gaining access to resources and protection from infanticide (see Bull and Baghurst, 1998; O'Connor and Shine, 2004; Sinn et al., 2008; While et al. 2009c). However, without birth order being a key predictor of the competitive asymmetries between siblings it is difficult to understand why competitive hierarchies establish within asynchronous but not synchronous litters (e.g., While and Wapstra, 2008). We suggest that while giving birth asynchronously does not change the competitive ability of offspring *per se*, it does change the level of competition within the litter, allowing for other traits, such as size, sex, paternity, or behavioural phenotype, to determine the outcome of such competition. For example, it has been suggested that an individual's relative size early in development, rather than its birth order, is most indicative of its position within the litter size hierarchy created by asynchronous birth and thus survival and growth (While and Wapstra, 2008). Considering the relatively modest sample size (despite high survival rates) and the potential multitude of causal factors on survival and growth such effects will be difficult to detect without experimental work. In line with this, future work should experimentally manipulate offspring size itself, utilizing allometric engineering techniques (e.g., Sinervo and Huey, 1990; Olsson et al., 2002), and compare its effects on size hierarchy establishment within both asynchronous and synchronous litters (using manipulation of synchrony; e.g., While and Wapstra, 2008). This would allow us to tease apart the role of asynchrony as a direct cause or a facilitator of sibling size hierarchies and thus the mechanism by which birthing asynchrony influences sibling competition.

In summary, survival and growth to maturity in *E. whitii* show inter- and intra-annual variation, the latter largely driven by variation in birth date. Importantly, an individual's survival rate over its second year of growth were largely independent of

survival over its first year, suggesting long-lasting effects of changes or perturbations in environmental or social conditions on the demography of populations. In contrast to many birds, birth order did not significantly impact on survival or growth, suggesting that the evolution of birthing asynchrony in this genus should be understood from a perspective of costs and benefits of the creation of sibling hierarchies *per se* rather than any direct effects of within-litter position on offspring fitness.

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